FIELDIANA: ZOOLOGY

A Continuation of the

ZOOLOGICAL SERIES

of

FIELD MUSEUM OF NATURAL HISTORY

VOLUME 51

FIELD MUSEUM OF NATURAL HISTORY
CHICAGO, U.S.A.

TABLE OF CONTENTS

* No. 16 incorrectly issued as vol. 51, no. 15. Correct the number to read 15 and pagination to read 169a through 178a.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 | July 25, 1966 | No. 1

A New Species of Lungless Salamander (Genus *Bolitoglossa*) from Panama

David B. Wake
Department of Anatomy, The University of Chicago
and
Arden H. Brame, Jr.
Department of Biological Sciences, University of Southern California

Several years ago Edward H. Taylor directed our attention to to several specimens of *Bolitoglossa* included in the Harold Trapido Panamanian collection at Field Museum of Natural History and suggested that they represented an undescribed form. Additional specimens of this strikingly distinct species have been collected on several occasions recently. All differ from other members of the genus in having bifurcated terminal phalanges. In reference to this unique structural feature the species may be known as

Bolitoglossa schizodactyla, new species. Figures 1 and 2.

Holotype.—FMNH 141241, an adult male from El Valle de Anton, 560 meters (1,837 feet), Provincia de Cocle, Panama, collected by Harold Trapido.

Paratypes.—PANAMA, Provincia de Cocle: El Valle de Anton, Finca Arce, collected by H. Trapido, G. Fairchild, and C. H. Michener (FMNH 142678, 152989-90); same locality, collected by P. Allen and H. Trapido (FMNH 152991); El Valle de Anton, 793 meters (2,600 feet) collected by G. Fairchild and H. Trapido (FMNH 152992-94). Provincia de Panama: Cerro la Campana, 850 meters (2,788 feet), collected by H. Trapido (FMNH 141240); 1 mile NW Posado San Antonio, collected by R. Dressler (UMMZ 124513); 3 miles NW Posado San Antonio, collected by O. J. Sexton (UMMZ 124514-15); vicinity of Altos de Pacora, E Cerro Jefe, 200-400

Library of Congress Catalog Card Number: 66-25494

FIG. 1. *Bolitoglossa schizodactyla*. FMNH 152989, an adult male from El Valle de Anton, Provincia de Cocle, Panama.

meters (650–1300 feet), collected by J. Barrat, Jr. (KUMNH 93511). Provincia de Bocas del Toro: Isla de Colon near La Gruta, 20 meters (65 feet), collected by C. W. Myers (KUMNH-CWM 2892); Peninsula Valiente at Bluefields, near sea level, collected by C. W. Myers (KUMNH-CWM 4259, 4290–4291).

Diagnosis.—A medium-sized species of *Bolitoglossa* (8 adult males: 38.3-60.9, mean 48.3 mm standard length; 9 adult females: 45.8–62.0, mean 56.4 mm standard length) distinguished from all other members of the genus by having bifurcated terminal phalanges on some to most digits of the hands and feet (fig. 2); distinguished further from most species by having very high numbers of vomerine teeth (totals 27–61, mean 39.8) and from all species by its unique color pattern of a well defined ventral yellow band, unmarked on the tail but interrupted by a median irregular black stripe on the belly, or immaculate whitish venter.

Description of the holotype.—Adult male, snout moderately long, truncate at tip. Well-developed mental hedonic gland, ovoid in shape with concave posterior margin, 2.2 mm long and 3.8 mm broad. Nostril small; labial protuberances of nasolabial groove moderate. Canthus rostralis of moderate length, slightly rounded. Standard

length 6.2 times head width; standard length 4.2 times snout-gular fold length. Shallow groove below eye extends almost full length of opening following curvature of eye, does not communicate with lip. Eye of moderate size, only slightly protuberant. Well defined post-orbital groove extends posteriorly from eye as shallow depression for 2.5 mm, proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as an indefinite depression parallel to and 3.7 mm anterior to gular fold. Vomerine teeth 47, in long double rows extending beyond the lateral borders of internal nares; rows only slightly curved posteriad medially. Maxillary teeth 61, extending posteriorly to a point about three-fourths through eye. Three premaxillary teeth, piercing lip. Tail long, 1.37 × standard length; slightly compressed; moderately constricted at base. No post-iliac gland. Limbs long, limb interval 1½; standard length 4.1 × right fore limb, 3.8 × right hind limb. Webbing of hands and feet almost complete with crescentic depressions between digital tips; tips of digits 2 through 4 plainly bifurcated although truncate in general outline. Parts of the terminal phalanges of fingers 2 and 3 and toes 2, 3, and 4 free from webbing. No obvious subterminal pads. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 2, 4, 5, 1.

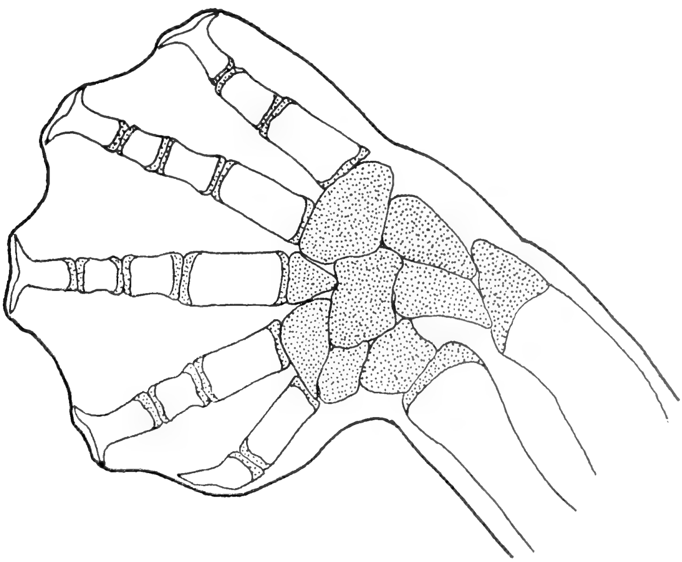


FIG. 2. Left hind foot of *Bolitoglossa schizodactyla*, FMNH 142678. Webbing outlined. Cartilage stippled.

Measurements (in mm).—Head width 8.1; snout to gular fold (head length) 12.0; head depth at posterior angle of jaw 4.3; eyelid length 3.7; eyelid width 1.8; anterior rim of orbit to snout 4.0; horizontal orbital diameter 2.7; interorbital distance 3.5; distance between vomerine teeth and parasphenoid tooth patch 0.6; snout to fore limb 15.2; distance separating internal nares 2.7; distance separating external nares 3.1; snout projection beyond mandible 1.4; snout to posterior angle of vent (standard length) 50.2; snout to anterior angle of vent 46.1; axilla to groin 26.0; tail length 69.0; tail width at base 4.1; tail depth at base 4.3; fore limb length 12.0; hind limb length 13.3; width of right hand 4.9; width of right foot 6.0.

Coloration (in alcohol).—Dorsal and lateral color of head, trunk, and tail black; dorsum of limbs medium brown with some pale mottling; feet light brown dorsally. Ventral color uniformly yellow-white from tip of tail to point just anterior to hind limb insertions where a median dark stripe appears in the center of the light band; stripe of irregular width, extends anteriorly to point just posterior to fore limb insertions. Yellow-white ventral band obscured by melanophores anterior to gular fold. Highly irregular line of intense black sharply sets off light ventral band from dorso-lateral dark coloration; demarcating line especially well developed on tail. Some brownish spots are scattered ventrally between the limb insertions and on the gular fold. Gular area grayish-brown.

Variation.—Although our sample is relatively small (17), the sexual dimorphism characteristic of the genus is apparent. Males average 48.3 mm standard length and females average 56.4 mm. These sizes are moderate within the genus. Sexual dimorphism is also apparent in limb length; males have hind limbs that range from 24.0 to 27.5 (mean 25.9) per cent of standard length, while those of females range from 20.4 to 25.9 (mean 23.5) per cent. Legs are long with limb intervals of from 1 to 2 (mean 1½) in males and from 1½ to 3½ (mean 2½) in females. Females have more maxillary and vomerine teeth than males, both absolutely and relative to size. Standard length is 5.7 to 6.2 (mean 6.0) × head width in males, 5.6 to 6.6 (mean 6.2) in females. Sexual dimorphism is not apparent in other dimensions.

There is some variation in foot shape, possibly an artifact of preservation. The feet are highly distinctive in shape with extensive webbing that is very obviously demarcated from the stout digits. The digital tips are broad, truncate, and usually somewhat concave, following the outline of the bifurcated terminal phalanges.

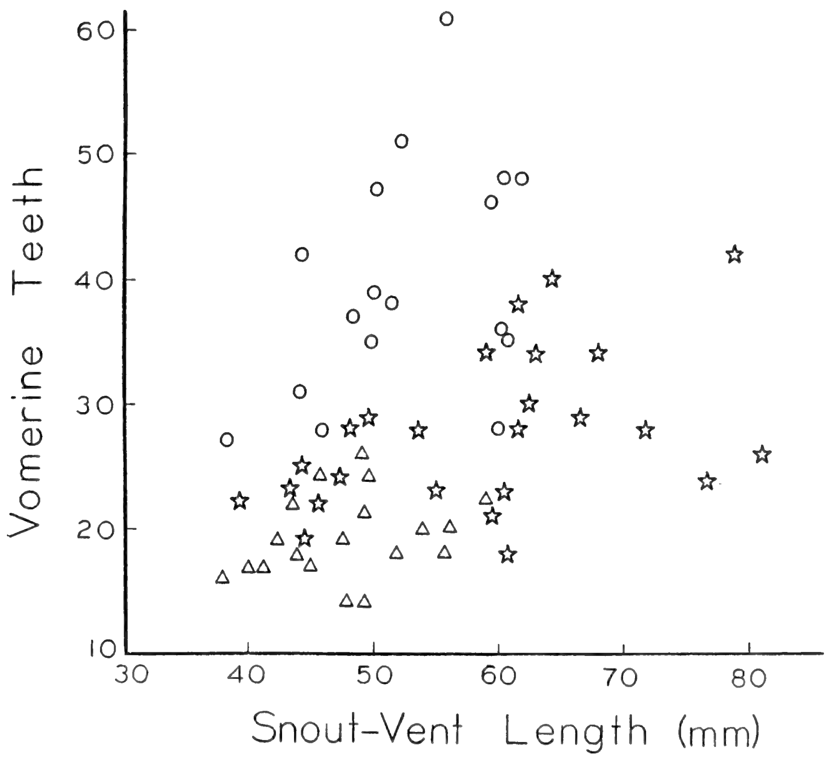


FIG. 3. Variation in vomerine dentition. Circle, *B. schizodactyla;* triangle, *B. vallecula;* star, *B. lignicolor.*

Some geographic variation in color pattern is apparent in the sample. Specimens from the southern and eastern parts of the range have a bright yellow ventral band which extends from the gular fold to the tip of the tail. The band is almost immaculate and has a shiny or enameled appearance. Trunk and tail melanophores partially obscure the band in some individuals. An irregular black stripe of variable width typically interrupts the yellow band midventrally; the stripe is broadest midway between the limb insertions and tapers to a point anteriorly and posteriorly (fig. 1). The brownish black coloration of the lateral surfaces is usually separated from the yellowish ventral coloration by a narrow, dark black border.

Specimens from the northern and western parts of the range usually lack well demarcated ventral bands. The venters are immaculate whitish with a slight reddish tinge. Numerous small pig-

mented dermal gland openings are evident. No midventral dark stripes or bordering dark lines are present.

Most of our sample resembles the holotype in dorsal coloration, but the specimens from Peninsula Valiente differ markedly from the others. In these atypical individuals an irregular mid-dorsal stripe of purplish black is bordered by irregular dorsolateral bands of light reddish yellow. Irregular lateral bands of purplish black to dark brown gradually blend into the light ventral color. Dorsal portions of the head and tail are mottled with reddish yellow and purplish black. The dorsal surfaces of the limbs are very dark purplish black.

Generally the dorsal and lateral ground color of melanic to purplish black in *B. schizodactyla* is covered and often largely concealed by varying amounts of metallic bronze and silver to grayish coloration (iridiophores and guanophores). This superficial coloration may be arranged in spots and blotches, or more or less evenly distributed over the lateral surfaces. The individuals available may be grouped as follows (based on dorsal and dorsolateral coloration): solid black (2), irregular purplish black mid-dorsal with reddish brown dorsolateral bands (3), large whitish to brownish blotches on a black background (4), whitish spots on a dark brown background (4), even gray suffusion (2), even brown suffusion (1).

Osteology.—Osteological information has been obtained from a single cleared and stained example (FMNH 142678). Frontal processes of the single premaxilla are relatively long with slight distal dilation. The processes remain separated for their entire lengths. Nasals are relatively large for the genus. Septomaxillae and prefrontals are absent. A large internasal space separates the vomers for their entire lengths, and the bones approach each other only posteriorly where the tooth bearing portions extend as processes toward the midline. Vomerine preorbital processes are large and long, extending beyond the lateral margins of the vomers proper. Very low otic crests are present. The opercular plates are oval and lack columellae. Vertebrae are amphicoelous with no sign of calcification of the intervertebral cartilages. No obvious boss is present on the atlas vertebra. There are 14 trunk, 1 sacral, 2 caudosacral, and 42 caudal vertebrae. Hypapophyses and basapophyses are absent. No tibial spurs are evident. Distal tarsals 4 and 5 are fused; eight cartilaginous elements occur in both carpus and tarsus. Terminal phalanges are bifurcated distally except on the first digit (see fig. 2).

Habitat.—The bifurcated terminal phalanges and the shape and webbing of the hands and feet suggest that *B. schizodactyla* is a

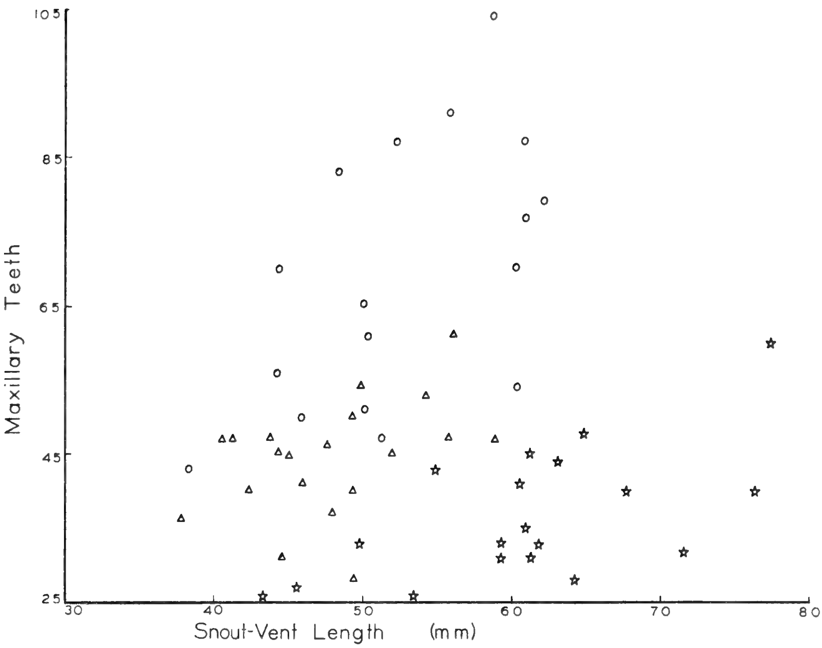


FIG. 4. Variation in maxillary dentition. Circle, *B. schizodactyla;* triangle, *B. vallecula;* star, *B. lignicolor.*

climbing or arboreal species. The La Gruta salamander was collected in vegetation, four feet above the ground. At least several of the specimens from El Valle de Anton (FMNH 142678, 152989–91) were collected in banana plants. The Bluefields specimens were found at night walking on palm and Helaconia leaves along a stream.

Relationships.—*B. schizodactyla* is apparently sympatric with *B. biseriata,* at least in central Panama. Several specimens of *B. biseriata,* collected from bananas at El Valle de Anton, are included in the Trapido collection. The two species occupy similar microhabitats, but are quite distinct structurally. *B. biseriata* is smaller, has fewer teeth, is lighter colored, and has flattened, more fully webbed hands and feet than *B. schizodactyla.*

B. schizodactyla is a remarkably distinct species and it is difficult to suggest its closest relatives. The shape of the terminal phalanges of the hands and feet and the highly distinctive color pattern are unique. Individuals of only five (*B. dofleini, B. lincolni, B. macrinii, B. morio, B. yucatana*) Guatemalan and Mexican species have as many as the mean number of vomerine teeth in *B. schizodactyla.*

The maximum number of vomerine teeth of *B. schizodactyla* (61) is exceeded only by *B. dofleini* (76 maximum). All of the above species differ markedly from *B. schizodactyla* in many characters and are not closely related to it.

B. lignicolor of Panama and Costa Rica, and *B. vallecula* of Colombia share characteristics with *B. schizodactyla* and may be close relatives. *B. lignicolor* resembles *B. schizodactyla* in size and habitus, and both species have extensively webbed hands and feet. Vomers of both species are well separated by large intervomerine fontanelles and have medially directed, spinous, toothed processes. Many differences distinguish the species. *B. lignicolor* has rather high numbers of vomerine teeth, but fewer than *B. schizodactyla* (fig. 3). *B. schizodactyla* has many more maxillary teeth (fig. 4). *B. schizodactyla* lacks vertebral basapophyses and prefrontal bones, both present in *B. lignicolor*, and has a somewhat broader head and longer limbs than has *B. lignicolor* (mean ratio of standard length to head width is 6.3 in males, 6.6 in females; mean limb interval is 3 in males, 3½ in females). *B. lignicolor* lacks bifurcated terminal phalanges. *B. schizodactyla* lacks the light dorsal wash or band, the dark trunk and

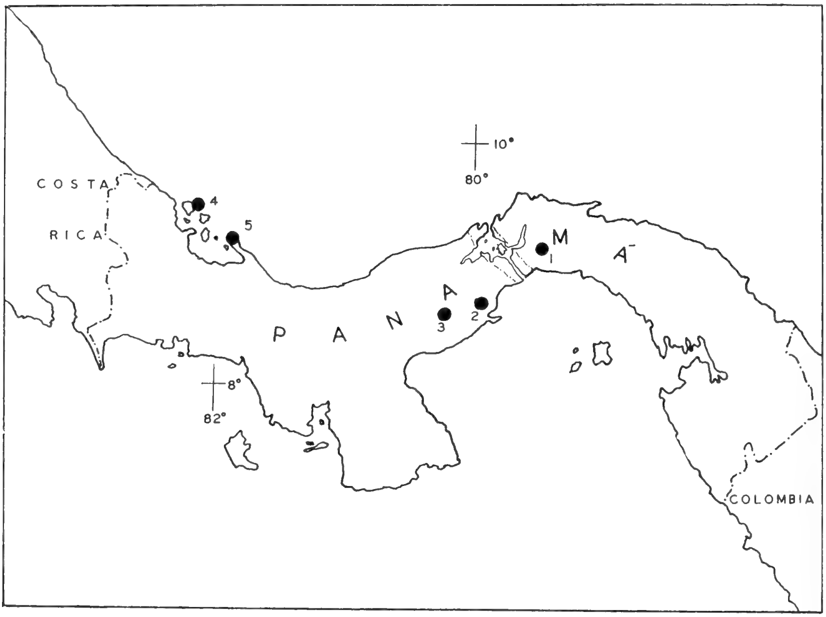


FIG. 5. Distribution of *B. schizodactyla* in Panama. 1. Cerro Jefe; 2. Cerro la Campana and Posada San Antonio; 3. El Valle de Anton; 4. La Gruta; 5. Peninsula Valiente.

tail venters, and the small ventral and limb guanophores of *B. lignicolor*.

B. schizodactyla resembles the somewhat smaller *B. vallecula* in having light colored trunk and tail venters and in general habitus. Ventral surfaces tend to be pinkish in *B. vallecula*, but bright yellow in *B. schizodactyla*. *B. vallecula* has incompletely webbed hands and feet and its truncated digits apparently lack bifurcated terminal phalanges. It also has fewer maxillary and many fewer vomerine teeth than *B. schizodactyla* (figs. 3 and 4). The head of *B. vallecula* is narrower (mean ratio of standard length to head width is 6.4 in males, 6.9 in females) and its limbs are slightly shorter (mean limb interval 2 in males, 3 in females) than those of *B. schizodactyla*. No skeletons of *B. vallecula* are available.

Other species which resemble *B. schizodactyla* include the poorly known Costa Rican forms *B. alvaradoi* and *B. arborescandens*.

TABLE I.—Data on *Bolitoglossa schizodactyla*.

Museum number		Snout-vent length	Axilla-groin	Head width	Hind limb length	Snout-gular fold	Limb interval	Tail length	Maxillary teeth	Vomerine teeth
KUMNH 93511	♂	60.9	34.0	10.4	16.0	16.0	2	66.8	77	35
FMNH 141241[1]	♂	50.2	26.0	8.1	13.3	12.0	1½	69.0	61	47
FMNH 142678	♂	50.1	27.3	8.2	12.9	12.1	1½	68.6	51	39
FMNH 152990	♂	50.0	27.1	8.1		11.7		67.0	65	35
FMNH 152989	♂	48.3	25.8	8.4	13.3	11.8	1	76.4	82	37
FMNH 152994	♂	44.4	24.0	7.8	11.2	11.1	2	60.0	70	42
UMNZ 124513	♂	44.1	23.8	7.2	11.4	10.0	1	51.8	56	31
UMMZ 124514	♂	38.3	17.7	6.5	9.2	10.5	1½		43	27
FMNH 152992	♀	62.0	33.2	9.5	13.3	13.9	2½	85.0	79	48
UMMZ 124515	♀	60.7	33.2	9.5	14.3	13.8	2½	60.2	87	48
KUMNH-CWM 4259	♀	60.3	33.9	9.1	12.3	13.0	3½	65.7	54	36
KUMNH-CWM 2892	♀	60.1	33.4	9.5	15.1	14.8	2	63.0	70	28
FMNH 152991	♀	59.2	32.5	10.0	14.8	14.8	2	70.8	104	46
KUMNH-CWM 4291	♀	55.9	31.4	9.3	12.6	13.8	3		91	61
FMNH 152993	♀	52.2	25.5	9.3	13.5	13.8	1½	68.0	87	51
FMNH 141240	♀	51.2	28.5	8.2	12.2	12.8	3		47	38
KUMNH-CWM 4290	♀	45.8	27.8	7.6	11.0	11.0	2½	49.2	50	28

[1] Holotype

Neither resembles *B. schizodactyla* in coloration, but they have extensively webbed hands and feet and are as large or larger than *B. schizodactyla*. These species lack truncated digital tips and have no indication of bifurcated terminal phalanges. *B. alvaradoi* resembles *B. schizodactyla* in head width but has fewer teeth. *B. arborescandens* has rather large numbers of teeth but has a narrower head than *B. schizodactyla*.

Several other species of *Bolitoglossa* (*biseriata, flaviventris, striatula*) have fully webbed hands and feet and light ventral coloration, but they differ so strikingly from *B. schizodactyla* in most other characters that close relationship is unlikely.

Distribution.—The species is known from western and central Panama (fig. 5). Dr. A. S. Rand (*in litt.*) has recently found the species on Barro Colorado Island.

Acknowledgements and abbreviations.—Material for the present study was made available through the courtesy of Robert F. Inger and Hymen Marx of Field Museum of Natural History (FMNH), Harold Trapido of the Rockefeller Foundation, Charles F. Walker of the University of Michigan Museum of Zoology (UMMZ), Curt R. Schneider and Eustorgio Mendez of the Gorgas Memorial Laboratory, and Charles W. Myers and William E. Duellman of the University of Kansas (KUMNH). We especially thank Edward H. Taylor for drawing our attention to the material and suggesting that it be described. We are grateful to Jay M. Savage and Robert F. Inger for their review of the manuscript and to William A. Bussing for photographic assistance. This investigation was aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago to the senior author, and from the National Institutes of Health (GM 12020) to William E. Duellman.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 NOVEMBER 28, 1966 No. 2

Evidence for Parthenogenesis in the Featherwing Beetles, with a Taxonomic Review of a New Genus and Eight New Species (Coleoptera: Ptiliidae).

HENRY S. DYBAS
ASSOCIATE CURATOR, DIVISION OF INSECTS
FIELD MUSEUM OF NATURAL HISTORY

INTRODUCTION

The new genus *Eurygyne* is a distinctive group of tiny featherwing beetles that is widespread in tropical and subtropical areas of the world. Though no members of the genus have been recorded previously from the United States, they seem to be rather abundant, especially in Florida where seven new species occur. The beetles are trim little forms, about 0.6 mm. long, that live in decaying organic materials in the floor stratum. There they presumably feed on spores and hyphae of fungi, as do other members of the family. In some situations they may become very numerous, though only one relatively huge egg is matured in the abdomen at a time.

Parthenogenesis has not been reported previously in the Ptiliidae, but evidence for complete parthenogenesis is presented for at least five of the eight new species of *Eurygyne*, and some possible reasons for its high incidence are suggested. One of the parthenogenetic new species has an anomalous geographical and ecological distribution in the United States, which is discussed later.

The Bahama Island form, in contrast to all the mainland species, is polymorphic with respect to the wings; most of the individuals have the expanse of the featherwing greatly reduced by the loss of most

Library of Congress Catalog Card Number: 66–29127

of the long marginal wing hairs, presumably as an adaptation against being passively wafted out to sea.

The eight new species are all from the United States and the adjacent Bahamas and from Bermuda. Other undescribed species occur in the New World and Old World tropics. Five nominal species from the Old World, described in the genus *Throscidium*, very probably belong to *Eurygyne* and are transferred to the genus though they cannot be identified from the descriptions.

Materials and Methods

In a group of insects as tiny as the Ptiliidae, appropriate techniques of collecting and sampling, of sorting and handling, and of study and illustration, are especially important. I plan to treat these techniques in a later paper; but it is adequate for the present to say that the taxonomic treatment in this paper is based on structures that cannot be studied from the traditional dry mounts, using stereoscopic microscopes and reflected light. There are external differences between the new species described in the following pages, but I have not used these differences for taxonomic purposes to any extent for two main reasons which apply to the Ptiliidae in general. First, the beetles are too small to study with the maximum magnifications and illumination practical with stereoscopic microscopes. Details of the antennae, legs, mouthparts, and other structures cannot be seen or analyzed well. Second, many of the differences that can be seen—slight species differences in color, pubescence, and general facies—cannot be accurately communicated to other biologists either through illustrations or through descriptions.

The only basis for a sound taxonomy in this genus, as in most Ptiliidae, lies in structures, like those of the antenna and spermatheca, that can only be studied and illustrated accurately from material mounted on microscope slides. In *Eurygyne,* the spermatheca has proved useful in differentiating the species. Constant differences characterize species that would be difficult to separate on the basis of external characters. A good example is furnished by *E. frosti* n. sp. and *E. suteri* n. sp. which are similar brown species externally, but which differ in the form of the spermatheca. A complex spermatheca like that in *intricata* is not easy to interpret and illustrate, since it is only about 0.1 mm. in greatest dimension. In the species with a simpler spermatheca, where slight variations in form can be readily detected, there is remarkably little variation within a species. In *frosti,*

lutea, and *fusca* (fig. 4), for example, I have examined, respectively, 370, 2,500, and 630 females without seeing any variations which did not fall clearly within one of the three spermathecal types.

This study is based upon about 11,400 specimens from the United States and another 600 specimens from the adjacent Bahamas and Bermuda. Except for *E. lutea* n. sp., all of the specimens of *Eurygyne* were studied on permanent slide preparations (Euparal mounting medium) or on temporary mounts (Hoyer's medium). In the case of *E. lutea*, the number of specimens was so large (in excess of 9,100) that they could not all be prepared as microscope slide mounts. In this case, the smaller lots were completely mounted, while the larger lots, all from Florida, were sampled after inspection in alcohol. Since *E. lutea* can be readily separated from the other presently known Florida species by its color and general facies, and by the triangularly acuminate coxal lamina of the hind leg, I believe the sampling procedure introduced no significant taxonomic or numerical error. About 2500 specimens (more than 25% of the entire sample) were studied on microscope slides, mostly in Hoyer's medium. Temporary media are useful for thinly sclerotized and lightly pigmented forms like most of the *Eurygyne* species, and they require much less time for slide preparation. The data on egg size and number were obtained from temporary mounts; the KOH stage in the preparation of permanent mounts destroys the egg. After study of the temporary slides, selected specimens were processed for permanent slides and the rest of the specimens were returned to alcohol vials.

Unless otherwise stated (e.g., "sifting . . .," "at light") the specimens reported in this paper were extracted by means of the insect (Berlese or Tullgren) funnel. The use of this technique permits, for the first time, the systematic sampling for Ptiliidae of the microhabitats in an area and the accumulation of adequate series for study.

Where the size of the series permits, specimens of the new species of *Eurygyne* described in this paper are to be deposited in the following collections: American Museum of Natural History (AMNH), British Museum (Natural History) (BM), Canadian National Collection (CNC), Illinois Natural History Survey (INHS), United States National Museum (USNM), and the collection of Eivind Sundt, Svartskog, Norway.

The Featherwing and Flight

Some data on the metathoracic wings are presented later in the paper and a preliminary description of the wing is desirable as it has

not been adequately described in the literature. The metathoracic wings in *Eurygyne* and in most Ptiliidae show a characteristic featherwing structure which is convergent in a number of unrelated groups of minute insects, notably Hymenoptera of the family Mymaridae. The wing (fig. 8) consists of a very narrow, heavily sclerotized basal strut and a much longer, narrow, membranous terminal portion which has no distinct wing veins but which has thickenings in the membrane. There is no thickened costal margin. The surface of the membrane has patches of microtrichia. The membrane of the wing is furnished with long marginal hairs which form the greater part of the expanse of the wing. There is an interruption in the array of marginal hairs, delimiting a terminal group from the proximal groups of the anterior and posterior margins. Just before their sockets in the membrane, the hairs are nearly transparent and are flexible (fig. 10a). When the wings are folded under the elytra, the hairs are appressed along the membrane and show through (in pale species) as dark vittae on each side. The wing folding pattern in *Eurygyne* is the same as described by Forbes (1926) for the genus *Acrotrichis*, which is in a different subfamily of Ptiliidae. There are no longitudinal folds as in most other beetles (Forbes, 1926), but only transverse folds, presumably because the membrane is very narrow. The first transverse fold is at the junction of the basal strut and the wing membrane. As in *Acrotrichis*, the folds are convex—concave—concave—convex (fig. 10b). This pattern may therefore be characteristic of most Ptiliidae except *Nossidium* and related genera, which have two parallel struts in the basal portion of the wing, a much wider wing membrane, correspondingly shorter marginal hairs, and a more complex wing-folding pattern (Forbes, 1926).

The convergent evolution of the featherwing in the most minute members of unrelated groups suggests that the featherwing structure is associated with the evolution of small size. It has been suggested by a number of authors (cf. Barber, 1924) that the featherwings function for passive dispersal, as in the ciliate seeds of plants.

Two main explanations for the evolution of the featherwing have been advanced. Rensch (1948) points out that in the evolution of small size in the Diptera, the thorax fills with flight muscles until finally a limit is reached when the thorax can no longer contain the necessary muscles and normal flight is no longer possible. He regards the convergent ciliated wing in Thysanoptera, Mymaridae, Trichogrammatidae, Ptiliidae, Sphaeridiidae, Clambidae, and minute Diptera, as an adaptation which enables the insect to make use of the viscosity of the air and to float.

Horridge (1956), on the other hand, points out that size is involved in the aerodynamics of an aerofoil like an insect wing. He concludes that the featherwings of Mymaridae and Ptiliidae are "operating in the range where the viscous drag forces are several times any possible lift forces. It is probable that they have abandoned altogether the aerofoil action and that they literally swim in the air." He points out that flight is still possible if there is some mechanism by which drag on the upstroke is less than that on the downstroke, for example, if the wings or bristles bend more easily on the upstroke than the down. In any case, such flight would be effective only over microdistances in still air, and passive dispersal by air-currents would seem to be the most important means of dispersal.

Eurygyne, new genus. Figures 1–14.

Throscidium auct. (*nec* Matthews 1872)

Type-species.—*Eurygyne intricata* new species.

Diagnosis.—A genus of Ptiliidae of oval, compact form with the hind coxae broadly laminate, nearly contiguous. Prosternum extremely short in front of the anterior coxae, which are very prominent. Mesosternum with a sharp median keel anterior to the mesocoxae; the keel does not reach the anterior border, which is delimited as a distinctly defined collar by a fine line. In one group of species, the collar extends onto the mesopleural humeri. The sutures lateral to the mesocoxae are straight, directed very slightly anteriorly, and are marked internally by a heavy endoskeletal ridge. Metasternum rather short, without 'metasternal lines'; produced between the hind coxae as a single pointed process. Abdomen without teeth at apex. Eyes emarginate behind and furnished with a dorsal flange, forming a pocket into which the anterior pronotal angles fit when the head is retracted. Femora of all legs narrowly laminate. Eyes well developed. Males unknown in some species. Distribution primarily pantropical and subtropical.

Description.—Form oval or elongate oval; head, pronotum, and elytra fairly smoothly contoured when body is contracted. Head large, broad, inserted into the pronotum to the eyes. Eyes large, prominent ventrally, emarginate behind, modified dorsally into a backward projecting flange which, together with the emargination, receives the anterior angles of the pronotum when the head is retracted. Antennae moderately long, 11-segmented; middle segments sub-cylindrical, elongate (shorter in *E. wagneri*), each slightly constricted at base and apex; segments 9–11 forming a loose, moderately enlarged club; segment 9, and more markedly segment 10, constricted beyond middle, vase-shaped. Mentum large, trapezoidal, sides slightly sinuate near base.

Pronotum broader than long, sides evenly curved; basal angles not noticeably prolonged; basal margin bisinuate near posterior angles, partly covering base of elytra and the triangular scutellum.

Elytra long, humeri with a slight angulation; epipleurae extending about half the elytral length.

Prosternum extremely short anterior to the coxae, which are very prominent.

Mesosternum short in front of coxae, extending little more than their greatest diameter; with a sharp median keel that does not reach the anterior border. The anterior border is delimited by a fine line as a distinctly defined collar. In one group of species (*wagneri* group), the collar extends onto the mesopleural humeri. Mesopleural humeri prominent, rounded, without a dentate projection. Mesocoxal acetabula broadly contiguous, the lateral sutures rather straight; directed slightly anteriorly, and marked internally by a heavy endoskeletal ridge (less developed in *steevesi* n. sp.). Metasternum short, about four times as broad as long; terminating between the hind coxae as a short pointed process (not bifurcate as in the Nanosellini). Metendosternite as in Figure 1b.

Abdomen nearly covered by the elytra, last segment partly exposed; 10-segmented; tergites I–V membranous or lightly sclerotized, II–V with the characteristic 'fingerprint' whorl pattern on each side; tergites I–VIII with a spiracle on each side; tergite VII with posterior margin micro-pectinate; tergite X well developed, separated from IX by a distinct straight suture, not dentate at apex. No sclerotized internal glands or row of 'glandular' pores (as in the Pterycini) visible. Sternite III, which is interpreted to be the first visible sternite, is somewhat carinate between hind coxae. Sternite IX in the female is an arcuate sclerite concealed by VIII; in the male (where the male sex is present) it can be detected internally as a spur projecting anteriorly to one side of the aedeagus.

Legs moderate in length; posterior coxae very broadly, subtriangularly laminate; anterior coxae relatively large, all femora with a narrow lamina. Anterior tibiae with one large spine at outer apex and two large spines before inner apex; tarsi slender, with slender subequal claws that bear a seta between.

Spermatheca tubular, varying from a simple U-shaped tube (cf. *E. lutea* n. sp.) to a highly coiled structure whose details are difficult to unravel (cf. *E. intricata* n. sp.).

Aedeagus (in species with males) tubular; no ventral hooks present.

Remarks.—The genus is distinctive and does not seem to be closely related to any other described genus in the Ptiliidae. In addition to the eight new species described in this paper from the eastern United States, the adjacent Bahama Islands, and Bermuda, five other nominal species that were formerly placed in *Throscidium* of authors (not Matthews, 1872) are tentatively assigned to *Eurygyne*. These species are *invisibilis* Nietner, *elongatula* Mots., *testaceum* Britten, *brunneum* Britten, and *nidicola* Paulian. The genus *Throscidium* Matthews, 1872, is thus left with only the two originally included species, *germaini* Matth., and *fairmairi* Matth. from Chile. The genus *Throscidium*, as restricted here by me, differs from *Eurygyne* in a number of characters, following Matthews' original description and figures

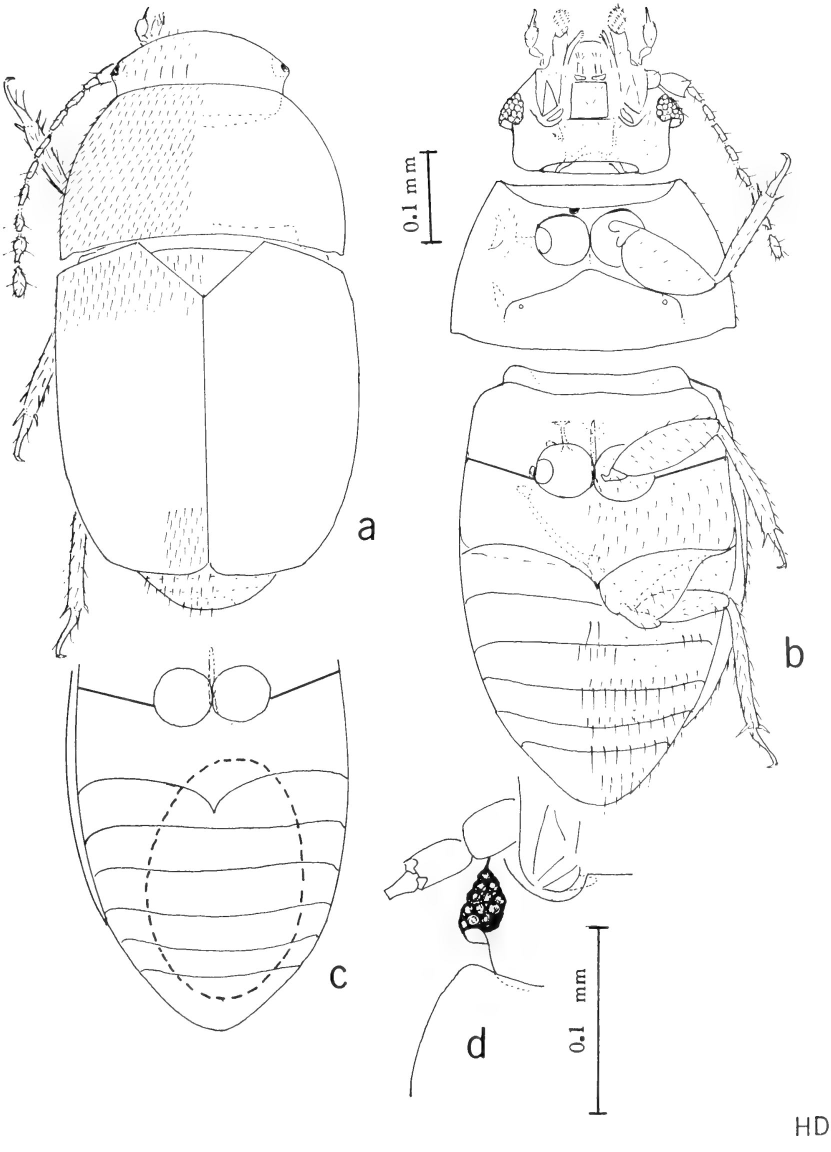


FIG. 1. *Eurygyne intricata* n. g. and sp. *a*, dorsal view. *b*, ventral view. *c*, egg. *d*, ventral view, enlarged, showing dorsal flange of eye.

(I have not seen any specimens): The pronotum has the posterior angles produced, the abdomen is tridentate at apex, the mesosternal carina is bifurcate anteriorly and reaches the collar, the femora are broadly laminate at apices, and the metasternum is proportionately longer. These differences clearly preclude the inclusion in *Throscidium* Matthews, 1872, of the species here assigned to *Eurygyne* n. g.

None of the five described species transferred from *Throscidium* can be certainly identified from the descriptions, but they are very probably congeneric with *Eurygyne*, and they thereby extend its distribution to Ceylon, the Seychelle Islands, Cape Verde Islands, Panama, Guatemala, and the Ivory Coast. There is also much unstudied material, mostly in Field Museum of Natural History, that supports the pattern of pantropical geographic distribution. There are extensive series from Middle and South America especially, but also from Angola, the former Belgian Congo, Thailand, and other regions. Judging from preliminary microscope-slide samples of these collections, the genus will contain numerous species once it is studied with appropriate techniques on a world-wide basis.

The eight new species fall into two well-defined species groups. The *intricata* group is characterized by the mesosternal collar being restricted to the neck and not extending onto the mesopleural humeri (fig. 6d). The included species are *intricata* n. sp., *lutea* n. sp., *fusca* n. sp., *frosti* n. sp., *suteri* n. sp., and *steevesi* n. sp. In the *wagneri* group, the collar extends onto the mesopleural humeri (fig. 6c). Included species are *wagneri* n. sp. and *contorta* n. sp.

The following is a brief historical resumé:

1857. Nietner described *Trichopteryx invisibilis* n. sp. from Ceylon.

1867. Wollaston recorded *Acrotrichis* (=*Trichopteryx*) *invisibilis* Nietner from Cape Verde Islands (based on an identification by Rev. A. Matthews).

1872. Matthews described *Throscidium* n. gen. based on *germaini* n. sp. and *fairmairi* n. sp. from Chile. No type of genus designated.

1884. Matthews transferred *Trichopteryx invisibilis* Nietner to *Throscidium*. *Acrotrichis elongatula* Motsch. (1868), described from Panama, was listed as a synonym.

1888. Matthews, in the Biologia Centrali Americana, listed the distribution of *Throscidium invisibile* Nietner as Guatemala, Panama, Ceylon, and Cape Verde Islands. A figure (Pl. III, fig. 25) of the general habitus was given.

1926. Britten described two new species from the Seychelle Islands: *testaceum* and *brunneum* n. spp.

1952. Paulian described *nidicola* n. sp. from the Ivory Coast.

KEY TO THE SPECIES OF *EURYGYNE* IN THE UNITED STATES AND THE ADJACENT BAHAMAS AND BERMUDA

1. Ptiliidae with the hind coxae contiguous, or nearly so, mesosternum with a sharp keel that does not reach the anterior margin, and with a sharply delimited anterior collar; abdomen not dentate at apex; prosternum extremely short in front of coxae; eyes emarginate behind and furnished with dorsal flange, receiving the anterior angles of the pronotum when head is retracted; elytra long . . . . *Eurygyne* Dybas, n. g. 2.

1a. Without the above combination of characters. . . . other genera of Ptiliidae (not keyed).

2. Mesosternal collar extending onto mesopleural humeri (fig. 6c). (*wagneri* group) 3.

2a. Mesosternal collar not extending onto mesopleural humeri (fig. 6d). (*intricata* group) 4.

3. Spermatheca as in figure 5b, c. Antennal segments shorter (fig. 5a); color pale; male with a fovea on the frons. . . . . *E. wagneri* Dybas, n. sp.

3a. Spermatheca as in figure 6b. Antennal segments longer (fig. 6a); color dark; male sex unknown. . . . . *E. contorta* Dybas, n. sp.

4. Spermatheca with numerous coils (fig. 2b, c). A yellow species; posterior margin of pronotum not sinuately notched near the angles; male sex known. *E. intricata* Dybas, n. sp.

4a. Spermatheca with only one or two loops; posterior margin of pronotum sinuately notched near the posterior angle; male sex unknown. . . . . 5.

5. Yellow; apex of hind coxal lamina acuminate; spermatheca as in figure 4c. *E. lutea* Dybas, n. sp.

5b. Brown or fuscous; apex of hind coxal lamina rounded, spermatheca not as in 5. . . . . 6.

6. Spermatheca as in figure 4a . . . . *E. fusca* Dybas n. sp.

6a. Spermatheca as in figure 4f . . . . *E. frosti* Dybas n. sp.

6b. Spermatheca as in figure 7a, b . . . . *E. suteri* Dybas n. sp.

6c. Spermatheca as in figure 7c . . . . *E. steevesi* Dybas n. sp.

Eurygyne intricata, new species. Figures 1a–d; 2a–e; 3a–c; 9; 11; 13.

Color yellow above and beneath; eyes dark; body covered with fine inclined golden setae. Posterior margin of pronotum not sinuately notched near posterior angles. Suture lateral to mesocoxae heavily ridged internally. Metathoracic wings polymorphic with respect to the number of marginal hairs. Form and chaetotaxy of antennae and of legs as figured (figs. 2a; 3a–c). Mesosternal collar not extending onto mesopleural humeri. Female with a distinctive, much coiled spermatheca (fig. 2b–c). Male aedeagus in the form of a tube (fig. 2d), its internal sac with

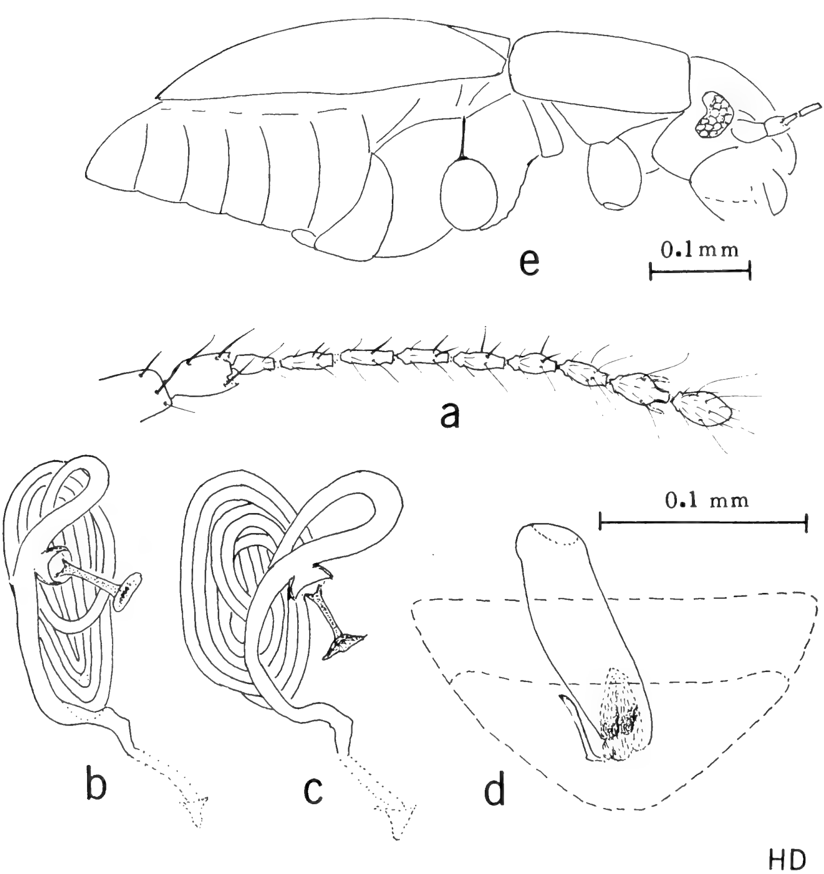


FIG. 2. *Eurygyne intricata* n. g. and sp. *a*, antenna, male. *b*, spermatheca, dorsal view. *c*, spermatheca, dorsal view, showing coils a little displaced. *d*, aedeagus, ventral view. *e*, lateral view, showing emargination in eye which receives the anterior angle of the pronotum when the head is retracted.

heavy sclerotizations which are visible through the walls of the aedeagus. No other secondary sexual modifications noted.

Measurements: About .52 mm. long from the anterior margin of the pronotum to the apex of the elytra; width about .33 mm. in slide-mounted specimens. In dry-mounted specimens, the total length from the tip of the retracted head to the apex of the abdomen is about .60 mm. long and .32 mm. wide.

Holotype.—A female, mounted on a microscope slide, from South Bimini Island, Bahama Islands, collected August, 1951, by C. and P. Vaurie. In the collection of the American Museum of Natural History.

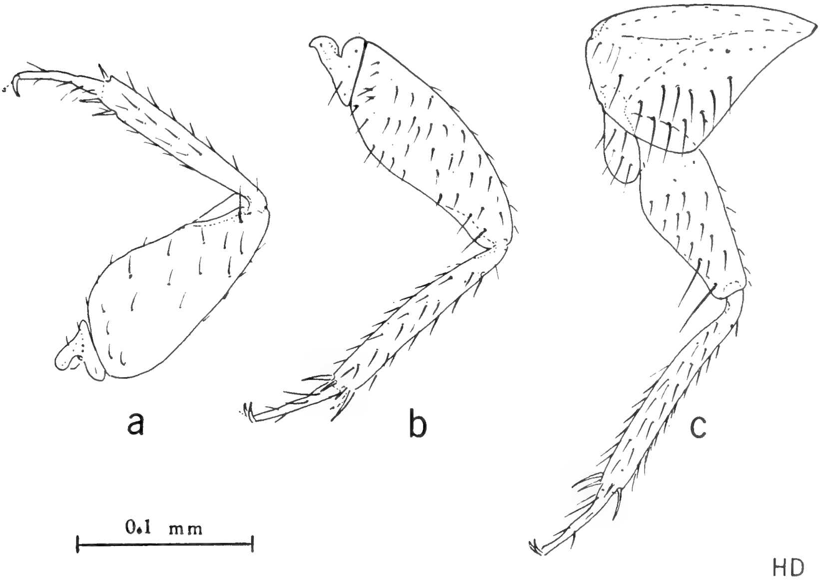


FIG. 3. *Eurygyne intricata* n. g. and sp. *a*, anterior leg, female, posterior face. *b*, middle leg, female, anterior face. *c*, posterior leg, female, anterior face.

Allotype.—A male, same data as the holotype. In the collection of the American Museum of Natural History.

Paratypes.—Same data as holotype, 116 ♀ ♀, 82 ♂ ♂; same data except June, 1951, collected by M. Cazier and C. and P. Vaurie, 59 ♀ ♀, and 58 ♂ ♂; same data except July, 1951, collected by C. and P. Vaurie, 158 ♀ ♀, 109 ♂ ♂. Paratypes in the collection of the American Museum of Natural History and Field Museum of Natural History.

Remarks.—*Eurygyne intricata* resembles *E. lutea* most closely in general appearance, but that species is slightly larger, the eyes are larger ventrally, and the posterior coxae are distinctly more acuminately triangular than in *intricata*. The specific name *intricata* refers to the intricately coiled spermatheca, which easily distinguishes this species from *lutea* and the other species in the *intricata* group.

The sex ratio, based on 582 sexed individuals, of which many are fragmentary, is 249 ♂ ♂ (43%) and 333 ♀ ♀ (57%). Of the 333 females, each of 76 (23%) had a single relatively huge egg in the abdomen. The egg measurement (from 24 measured eggs) averages .31 by .18 mm. The size of the egg precludes the maturation of more than one egg at a time in the abdomen.

The metathoracic wings show an unusual kind of polymorphism hitherto unreported in the family. In most of the individuals there is a great reduction in the number of long marginal wing hairs that normally account for much the greater part of the total wing expanse in the Ptiliidae. An extremely reduced wing of *intricata* has a fairly normal basal strut and terminal membrane, but the hairs in the terminal group may number only ten or less (fig. 9) whereas seven individuals with well-developed wings (of a sample of 107) averaged 50 hairs (fig. 11). Variation in the number of hairs in the anterior and posterior proximal groups was concomitant with that of the terminal group. This strong polymorphism and great variability contrasts sharply with *E. lutea* (fig. 11) and the other mainland *Eurygyne*, all of which have full complements of marginal wing hairs and show little variability. Additional remarks on the wing polymorphism are deferred until the *Discussion*.

There is no obvious reason, unless it be ecological, why this species should not yet be found on the Florida mainland. South Bimini Island is only 60 miles off the coast of Florida, and the prevailing southeast breezes during the summer should facilitate dispersal of the fully-winged individuals of *intricata* to suitable habitats on the Florida coast.

A description of the type locality and collecting activities is given by Vaurie (1952). Collected along with *Eurygyne intricata* were 12 female specimens of *lutea*, one female of *frosti*, large series of an *Acrotrichis* sp., several species of *Actidium*, and a few *Micridium* sp. According to Vaurie (1952), "The Ptiliidae were the most numerous Coleoptera taken. So many of them were in the debris from the Berlese funnels that when the alcohol vials in which they were collected were shaken the beetles formed a black cloud."

Eurygyne lutea, new species. Figures 4c, d; 8; 10a, b; 11; 12.

Color yellow above and beneath. Body covered with fine inclined golden setae. Similar to *E. intricata* in form and in general appearance, but slightly larger and the eyes more prominent ventrally. Collar of mesothorax not extending onto humeri. The apex of the triangular metacoxal lamina is more acute than in *E. intricata*, and in the other species of the genus. Female spermatheca a simple U-shaped tube of diagnostic form (fig. 4c, d). Male sex unknown.

Measurements: in slide prepared specimens, about .58 mm. long from the anterior margin of the pronotum to the apex of the elytra. In dry-mounted specimens, the total length from the tip of the retracted head to the apex of the abdomen is .58 to .63 mm.; the width is .32 to .34 mm.

Holotype.—A female, mounted on a microscope slide, from Palma Vista Hammock, Everglades National Park, Dade County, Florida,

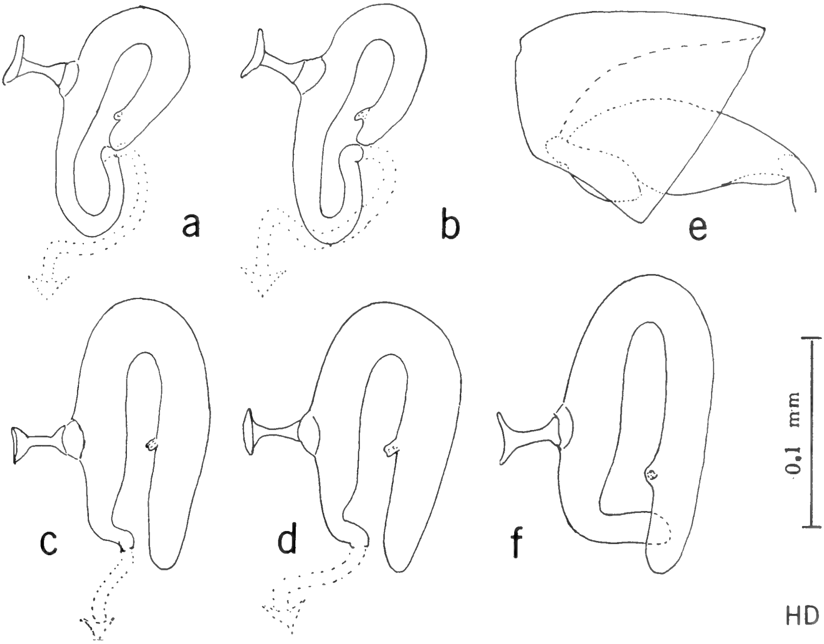


FIG. 4. *a*, *Eurygyne fusca* n. sp., spermatheca (Alabama) ventral view. *b*, spermatheca (Illinois), ventral view. *c*, *Eurygyne lutea* n. sp., spermatheca (Alabama), ventral view. *d*, spermatheca (Florida), ventral view. *e*, posterior coxa. *f*, *Eurygyne frosti* n. sp., spermatheca, ventral view.

collected August 27, 1965, by Walter Suter, "floor-litter at buttress of large tree." In the collection of Field Museum of Natural History.

Paratypes.—414 females, same data as holotype. In the collection of Field Museum of Natural History.

Other records.—FLORIDA: ALACHUA COUNTY, Island Grove, palmetto-cypress-maple swamp, Aug. 22, 1965, W. Suter leg., "litter at log with *Passalus*," 19 ♀ ♀; "litter in palm-cypress buttress," 31 ♀ ♀; "debris under palmetto frond," 3 ♀ ♀; same, but at Orange Grove, H. R. Steeves, Jr. leg., "debris at swamp edge," 32 ♀ ♀; 5 miles E. of Micanopy, Aug. 22, 1965, W.S.[1] leg., "peripheral litter on sawdust pile in buttress of oak," 38 ♀ ♀; Gainesville, pine-yellow poplar-magnolia ravine forest, Aug. 22, 1965, W.S. leg., "debris in buttress of yellow poplar," 6 ♀ ♀; "debris at pine buttress," 25 ♀ ♀; "forest floor at log in lowland along stream," 108 ♀ ♀. BAKER COUNTY,

[1] Hereafter W.S. = Walter Suter.

5 miles N. of Macclenny, Aug. 2, 1965, H.R.S.[1] leg., "debris under palmettos and scrub," 2 ♀ ♀; Aug. 18, 1965, W.S. leg., "pine-palmetto buttress debris on river bank," 1 ♀; "debris in pseudo fork of swamp white oak," 1 ♀; "bush fork accumulation," 3 ♀ ♀; Aug. 21, 1965, "bush fork accumulation," 1 ♀. CALHOUN COUNTY, 1 mile N.W. of Blountstown, July 25, 1965, W.S. leg., multiple sawdust piles about 15 years old near swamp forest, "sawdust and litter from periphery under magnolia shrubs," 12 ♀ ♀; "outwash leaf-litter at edge of sawdust pile," 17 ♀ ♀; Scott's Ferry, "floor-litter under oak and magnolia shrubs in pine woods," 3 ♀ ♀. COLLIER COUNTY, East of Ochopee, cypress-palmetto-maple swamp, June 17, 1965, W.S. leg., "debris in Cypress buttress," 1 ♀; Collier-Seminole State Park, Royal Palm Hammock, Aug. 28, 1965, W.S. leg., "litter under ferns and bushes," 2 ♀; same, H.R.S. leg., "debris under banana trees," 1 ♀; Monroe Station, 3 miles east, cypress swamp, Aug. 28, 1965, W.S. leg., 72 ♀ ♀; same, H.R.S. leg., "hammock-like swamp grass litter," 8 ♀ ♀. DADE COUNTY, Florida City, pine-palmetto woods, Aug. 26, 1965, W.S. leg., "debris at pine buttress," 109 ♀ ♀; "debris under banana tree," 74 ♀ ♀; same, no microhabitat data, 74 ♀ ♀; Everglades National Park, Palma Vista Hammock, Nov. 26, 1961, J. Wagner[2] leg., "floor duff," 26 ♀ ♀; June 18, 1965, W.S. leg., "floor pocket," 25 ♀ ♀; "debris at buttress of gumbo-limbo," 6 ♀ ♀; "litter at logs with polypore fungi," 46 ♀ ♀; "stage 3 branch," 9 ♀ ♀; "floor litter," 95 ♀ ♀; "litter in small limestone sink," 43 ♀ ♀; "floor litter at log," 376 ♀ ♀; same, no microhabitat data, 180 ♀ ♀; H.R.S. Jr. leg., "forest floor debris at fallen logs," 499 ♀ ♀; "forest floor debris pockets, some with wood," 358 ♀ ♀. DIXIE COUNTY, Old Town, June 16, 1965, W.S. leg., "palmetto stump," 1 ♀. FRANKLIN COUNTY, Buck's Siding, July 21, 1965, W.S. leg., old sawdust pile near stream, "sawdust under shrubs and briars at edge of north side of old sawdust pile," 21 ♀ ♀; "litter under palmetto, sawdust pile," 2 ♀ ♀; "litter under bushes on edge of sawdust pile," 12 ♀ ♀. GULF COUNTY, 6 miles N. of Weweahitchka, July 25, 1965, W.S. leg., "sawdust and leaves under bushes at edge of sawdust pile," 60 ♀ ♀; "oak logs, stage 3," 4 ♀ ♀. HIGHLANDS COUNTY, Highlands Hammock State Park, Aug. 23–24, 1949, H. S. Dybas leg., 9 ♀ ♀; "in decaying grass pile," 1 ♀; "leaf litter," 1 ♀; June 19, 1965, W.S. leg., "palm stump," 1 ♀; Aug. 24, 1965, W.S. leg., "oak log with *Passalus*," 2 ♀;

[1] Hereafter H.R.S.=H. R. Steeves, Jr.

[2] Hereafter J.W.=J. Wagner.

"debris at buttress of cypress and oak," 1 ♀; "floor litter from drainage depression," 2 ♀ ♀; "pine-magnolia pseudo fork debris," 4 ♀ ♀; H.R.S. leg., "debris inside palm logs," 4 ♀ ♀; "debris in pine-magnolia buttress," 5 ♀ ♀; "forest floor debris," 3 ♀ ♀; "cypress swamp debris at forest floor and at buttress," 50 ♀ ♀; Archbold Biological Station, June 12, 1955, H.S.D.[1] leg., "decayed ditch dredgings," 59 ♀ ♀; same, 20 ♀ ♀; same, 12 ♀ ♀; same, no microhabitat data, 5 ♀ ♀; "oak-pine leaves compost," 1 ♀; Nov. 15, 1959, S. W. Frost leg., "at light," 4 ♀ ♀; "Parker Islands" east of Lake Placid, Aug. 25, 1965, H.R.S. leg., "fern rhizome and woody debris, magnolia swamp," 58 ♀ ♀; "forest floor debris, pine woods on lake shore," 286 ♀ ♀; W.S. leg., "litter at log, pine grove on lake shore," 89 ♀ ♀; "debris among fern rhizomes," 86 ♀ ♀; "wet palm-palmetto pseudo fork," 188 ♀ ♀; "stage 4 log," 19 ♀ ♀; "litter under ferns at oak," 49 ♀ ♀; "stage 3 log," 1 ♀; "*Osmunda* rhizome clump," 1 ♀; "debris at magnolia buttress," 1 ♀; "floor debris at fern rhizome," 8 ♀ ♀; no microhabitat data, 15 ♀ ♀; Aug. 26, 1965, W.S., "floor debris at logs," 50 ♀ ♀; H.R.S. leg., "fern rhizome and woody debris," 97 ♀ ♀; Venus, 4 miles W., Fish Eating Creek, Aug. 25, 1965, W.S. leg., "grassy compost mixed with cypress, near water," 15 ♀ ♀; H.R.S. leg., "grass mat at edge of cypress swamp," 45 ♀ ♀; same, 20 ♀ ♀; southwest shore of Lake Istokpoga, June 14, 1955, H.S.D. leg., "debris at base of cypress on lake shore," 1 ♀; southwest shore of Lake Clay, near Lake Placid, June 14, 1955, H.S.D. leg., "leaf-litter in thicket," 2 ♀ ♀; same, 5 ♀ ♀. JEFFERSON COUNTY, 1 mile east of Capps, July 24, 1965, W.S. leg., "floor litter at log on slope to floodplain of pine-oak-sycamore forest," 1 ♀. LEE COUNTY, Fort Meyers, June 17, 1965, W.S. leg., "punk tree-buttress debris," 9 ♀ ♀. LEON COUNTY, 5 miles west of Iamonia (Tall Timbers Research Forest), August 4, 1965, W.S. leg., "debris under beech logs," 1 ♀; "damp leaf litter," 2 ♀ ♀; south of Chaires, July 19, 1965, W.S. leg., "sawdust under bush," 2 ♀ ♀; Aug. 14, 1965, W.S. leg., sawdust pile, "sawdust from bush-raspberry peripheral area of pile," 1 ♀; Aug. 29, 1965, W.S. leg., "moss on logs and in buttress in adjacent swamp," 1 ♀; same, H.R.S. leg., "sawdust pile," 4 ♀ ♀; Coe's Landing, Lake Talquin, 10 miles west of Tallahassee, Aug. 17, 1965, W.S. leg., "debris from walnut buttress near lake," 2 ♀ ♀. LEVY COUNTY, Manatee Springs State Park, Sept. 12, 1959, W.S. leg., "pine-litter," 13 ♀ ♀; Gulf Hammock, June 16, 1965, W.S. leg., "litter at moss covered logs," 23 ♀ ♀; "magnolia(?) stump," 3 ♀ ♀; "pine buttress," 1 ♀;

[1] Hereafter H.S.D.=Henry S. Dybas.

"palmetto and log litter," 12 ♀ ♀; Bronson, June 27, 1965, W.S. leg., "live-oak tree hole," 1 ♀. LIBERTY COUNTY, Sumatra, July 21, 1965, W.S. leg., "sawdust under small shrubs and raspberry on 15-year-old sawdust pile," 5 ♀ ♀. MADISON COUNTY, 5 miles east of Lee, July 31, 1965, W.S. leg., "walnut branches with *Passalus*," 10 ♀ ♀; "pine buttress," 5 ♀ ♀; 4 miles west of Madison, Aug. 21, 1965, W.S. leg., "floor litter at stage 3 pine(?) log," 3 ♀ ♀; "oak buttress," 5 ♀ ♀; Mefford's Cave, Aug. 14, 1965, S. Peck leg., "debris," 1 ♀. MARION COUNTY, 2 miles west of Silver Springs, June 27, 1965, W.S. leg., "palm log with *Fomes* fungus," 5 ♀ ♀; "sweet gum(?) log," 1 ♀; "palmetto stump," 1 ♀. MONROE COUNTY, 5 miles north of Flamingo, Everglades National Park, Aug. 27, 1965, W.S. leg., "grassy compost in shade of bush, sawgrass area," 2 ♀ ♀; "litter under shrubs along canal and Snake Bight Trail," 11 ♀ ♀. ORANGE COUNTY, Orlando, July 31, 1965, W.S. leg., "pine buttress debris, pine-palmetto area," 93 ♀ ♀; "grassy compost in field," 10 ♀ ♀; "debris in buttress of cypress," 35 ♀ ♀; "floor litter under bush, cypress area," 18 ♀ ♀; Aug. 22, 1965, W.S. leg., "debris in pine buttresses," 436 ♀ ♀; "grassy compost on edge of swamp," 178 ♀ ♀; H.R.S. leg., "pine-cypress swamp, buttress and stump debris," 382 ♀ ♀. OSCEOLA COUNTY, St. Cloud, Dec. 26, 1965, S.P.[1] leg., "debris under dead oak tree bark," 1 ♀. PINELLAS COUNTY, Tarpon Springs, June 16, 1965, W.S. leg., "cypress stump," 1 ♀. SARASOTA COUNTY, Myakka River State Park, June 16, 1965, W.S. leg., "palmetto," 3 ♀ ♀. SEMINOLE COUNTY, 3 miles north of Longwood, Aug. 23, 1965, W.S. leg., "pine-buttress," 241 ♀ ♀; "oak buttress," 480 ♀ ♀; "stage 3 linden branch with termites," 37 ♀ ♀; "debris in oak buttress," 232 ♀ ♀; "debris in oak-palmetto pseudofork," 210 ♀ ♀; "debris in oak-palm pseudo-fork," 564 ♀ ♀; same, H.R.S. leg., "rotten log, palmetto debris," 725 ♀ ♀; "debris, pine, palmetto buttress," 610 ♀ ♀. SUWANEE COUNTY, Falmouth, July 31, 1965, W.S. leg., "litter under oak leaves on edge of sawdust pile in oak woods," 15 ♀ ♀. TAYLOR COUNTY, Athena, Sept. 12, 1959, W.S. and J.W. leg., "pine litter," 16 ♀ ♀; Steinhatchee, 3 miles west, July 3, 1965, W.S. leg., "palm log on swamp floor," 1 ♀. VOLUSIA COUNTY, Osteen, Sept. 13, 1965, W.S. and J.W. leg., "pine litter," 3 ♀ ♀; Enterprise, Sept. 13, 1959, W.S. and J.W. leg., "pine debris," 15 ♀ ♀; 2 miles southwest of Enterprise, July 31, 1965, W.S. leg., "pine buttress, oak-pine forest," 15 ♀ ♀; "oak log and floor debris, oak-pine-palmetto woods," 1 ♀; "debris in oak buttress and fork," 2 ♀ ♀; "oak-palmetto pseudofork,

[1] Hereafter S.P.=S. Peck.

oak-pine forest," 85 ♀ ♀; "oak log, stage 3, on floor of oak-palmetto swamp," 9 ♀ ♀; "oak branch, stage 3, oak-palmetto swamp," 7 ♀ ♀; "palmetto axil debris, oak-palmetto swamp," 14 ♀ ♀; Aug. 23, 1965, "decaying crown of fallen palm," 2 ♀ ♀; "oak log, stage 3," 110 ♀ ♀; "oak tree hole," 16 ♀ ♀; "oak branch, stage 3," 13 ♀ ♀; "oak shrub pseudofork, up-land," 84 ♀ ♀; "litter under magnolia bush," 49 ♀ ♀; "palm log, lowland," 4 ♀ ♀; H.R.S. leg., "oak log," 37 ♀ ♀. WAKULLA COUNTY, 2 miles north of Sopchoppy, July 21, 1965, W.S. leg., "buttress of pine stump in pine woods," 1 ♀.

GEORGIA: BRANTLEY COUNTY, 1 mile east of Nahunta, Aug. 18, 1965, W.S. leg., "debris at pine buttress," 1 ♀. CHARLETON COUNTY, St. George, Aug. 18, 1965, W.S. leg., "litter under chicken feathers on edge of 20-year-old sawdust pile," 1 ♀; "debris at pine buttress at edge of sawdust pile," 64 ♀ ♀; "litter under raspberry at edge of sawdust pile," 6 ♀ ♀; 6 miles south of St. George, Aug. 18, 1965, W.S. leg., "debris in pseudofork of magnolia(?)-yellow poplar," 1 ♀; "debris at pine buttress with stage 3 oak log at swamp edge," 1 ♀. CLINCH COUNTY, DuPont, July 27, 1965, W.S. leg., "litter on sawdust pile under fern and pine," 12 ♀ ♀; "debris at pine buttresses in woods near sawdust pile," 2 ♀ ♀. DECATUR COUNTY, 1 mile northwest of Climax, limestone sink at "The Cave," Aug. 12, 1965, W.S. leg., "debris in pine buttress," 35 ♀ ♀. GLYNN COUNTY, 5 miles south of Thalman, Aug. 18, 1965, W.S. leg., "pine-oak pseudofork," 1 ♀; Jekyll Island, pine-oak-palmetto tangle near center of island, Aug. 18, 1965, W.S. leg., "oak buttresses," 1 ♀. GRADY COUNTY, 5 miles southwest of Beachton, Aug. 4, 1965, W.S. leg., "large wet oak log, stage 3," 1 ♀. LOWNDES COUNTY, 2 miles east of Valdosta, July 27, 1965, W.S. leg., "debris at pine buttress," 9 ♀ ♀.

ALABAMA: MOBILE COUNTY, Mobile, June 16, 1959, J.W. leg., "leaf-litter, swamp forest," 3 ♀ ♀; June 6, 1960, W.S. and J.W. leg., "pine duff, swamp," 1 ♀; Sept. 10, 1959, W.S. leg., "magnolia leaf-litter," 3 ♀ ♀; Sept. 11, 1959, W.S. leg., "maple-oak litter," 78 ♀ ♀; "pine litter, swamp forest," 22 ♀ ♀.

LOUISIANA: JEFFERSON PARISH, Harahan, Aug. 24, 1944, H.D. leg., "in decaying magnolia seed pods," 1 ♀; Sept. 26, 1944, F. Werner leg., "rotten magnolia fruit," 5 ♀ ♀. ASCENSION PARISH, Gonzales, Oct. 16, 1953, H.S.D. leg., "in wood-borer sawdust beside hollow, cut oak log," 1 ♀.

BERMUDA: HAMILTON PARISH, Hamilton Sound, Jan. 3, 1964, W. and J. H. Suter leg., "berlesed palmetto crotches," 1 ♀; same, Dec. 30, 1963, "leaf-litter, scrub forest," 1 ♀.

BAHAMA ISLANDS: South Bimini Island, June, 1951; M. Cazier and C. and P. Vaurie leg., 4 ♀ ♀; same locality, July, 1951, C. and P. Vaurie leg., 8 ♀ ♀ (1 callow).

Remarks.—*Eurygyne lutea* is most similar to *E. intricata* in general appearance, but differs conspicuously in the form of the spermatheca and, externally, in its slightly larger size, more prominent development of the eyes ventrally, and in the more acute apex of the triangular lamina of the posterior coxae.

In the series of 2,500 females examined on microscope slide mounts, there is very little variation in the spermatheca apart from variations that can be attributed to accidents of preparation or to the distorted condition of weakly sclerotized, callow individuals. All of the well-prepared specimens could be definitely assigned on the basis of spermathecal form alone without difficulty.

No males have been discovered in the large sample, which consisted of 9,164 specimens collected in 169 lots in many localities in four states and in the adjacent Bahamas and in Bermuda. The collections were made in eight separate months of the year as well. These data strongly support the hypothesis that *lutea* is a parthenogenetic species in its present recorded range. The species probably has a wider distribution in Middle America and in the West Indies, at least, but the collections of *Eurygyne* from these regions have not yet been studied in detail.

Unlike the situation in *Eurygyne intricata*, eggs were only rarely detected in the very large sample of *lutea* (about 2,500 females) mounted in Hoyer's medium on microscope slides. It is the developed chorion which shows through the abdomen and outlines the egg in such preparations. The large yolk granules can also be detected in many cases. In two females, each with a single, relatively huge egg, the eggs measured .28 by .16 mm. and .32 by .18 mm., or approximately one-half the total length of the beetle.

No reduction or polymorphism of the wings was noted in the extensive sample. In 123 females, representing 27 collections from 11 counties in Florida and 2 in Georgia, the number of marginal wing hairs in the terminal group (fig. 8) ranged from 53–61, with a mean of 57 (fig. 11). Three *lutea* females from South Bimini Island, Bahamas, had a range of from 57–59 hairs, which is well within the range of variation of the mainland sample.

Eurygyne fusca, new species. Figures 4a, b; 12.

Color brown; antennae, mouthparts, legs, yellow; body covered with fine inclined yellow setae. Collar of mesothorax not extending onto humeri. Posterior

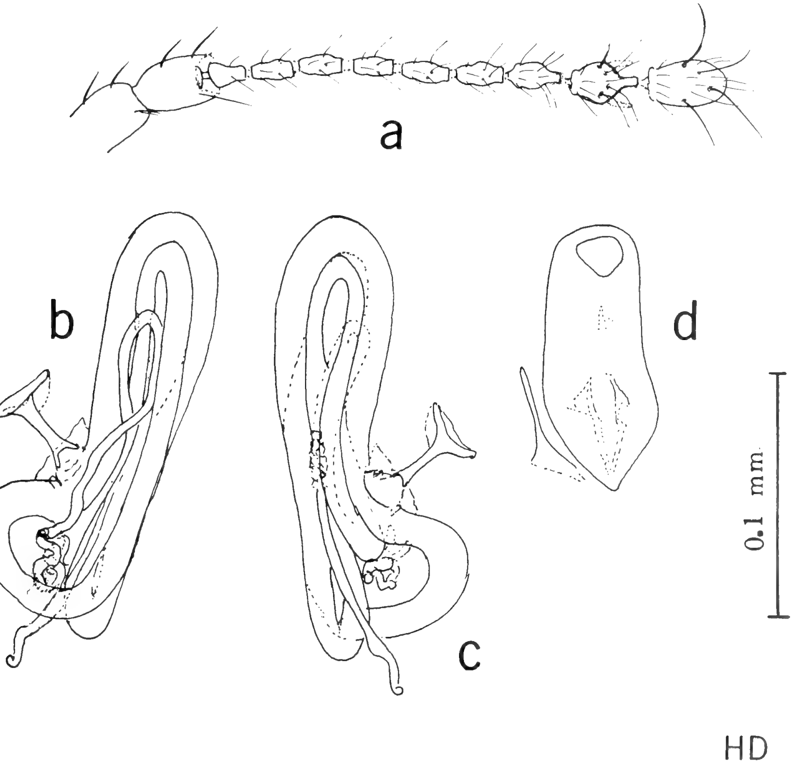


FIG. 5. *Eurygyne wagneri* n. sp., *a*, antenna, female. *b*, spermatheca, ventral view. *c*, spermatheca, dorsal view. *d*, aedeagus, ventral view.

margin of pronotum sinuately notched near posterior angles. Suture lateral to mesocoxae heavily ridged internally. Females with spermatheca of diagnostic form (fig. 4a, b). Male sex unknown.

Measurements: In dry-mounted specimens, the total length, including retracted head and apex of abdomen, is .62–.66 mm.; the width is .31–.32 mm.

Holotype.—A female, mounted on a microscope slide, from Fieldon, Jersey County, Illinois, collected Aug. 3, 1959, by W. Suter and J. Wagner, in "sawdust pile." In the collection of Field Museum of Natural History.

Paratypes.—189 ♀♀, same data as holotype. In the collection of Field Museum of Natural History.

Other records.—ILLINOIS: same locality as type, Nov. 3, 1965, H.S.D. leg., "in flight over large sawdust pile, 2:30 PM (CST), overcast," 1 ♀.

ALABAMA: TALLADEGA COUNTY, McElderry, Sept. 20, 1959, W.S. leg., "berlesed sawdust pile," 5 ♀ ♀; MARSHALL COUNTY, Guntersville, June 22, 1959, W.S. and J.W. leg., "berlesed sawdust pile," 1 ♀; BIBB COUNTY, Brent, Sept. 9, 1959, W.S. leg., "sawdust pile," 35 ♀ ♀.

FLORIDA: LEON COUNTY, Tallahassee, Sept. 15, 1944, J. H. Davis leg., "berlesed oak-pine leaves compost," 6 ♀ ♀ +7 fragm. ♀ ♀, 27 unsexed; HIGHLANDS COUNTY, Archbold Biological Station near Lake Placid, Nov. 15, 1959, S. W. Frost leg., "at light," 1 ♀. JEFFERSON COUNTY, Monticello (6 miles W.), July 24, 1965, W.S. leg., "beech tree-hole," 1 ♀; same, "sawdust pile—sawdust under logs," 195 ♀ ♀; same "litter pocket at logs on sawdust pile," 92 ♀ ♀.

MISSISSIPPI: JACKSON COUNTY, 4 miles east of Ocean Springs, Oct. 15, 1953, H.S.D. leg., "sifting floor litter in mixed pine-deciduous forest," 4 ♀ ♀.

MARYLAND: HOWARD COUNTY, Woodstock, July 26, 1959, W.S. and J.W. leg., "sawdust," 1 ♀; GARRETT COUNTY, 3 miles west of Deer Park, July 25, 1959, W.S. leg., "sawdust," 2 ♀ ♀.

PENNSYLVANIA: WESTMORELAND COUNTY, Seward, July 28, 1959, W.S. leg., "sawdust," 25 ♀ ♀; south of Seward, July 24, 1959, J.W. leg., "sawdust pile," 3 ♀ ♀.

TENNESSEE: McNAIRY COUNTY, Selmer, Sept. 9, 1959, W.S. leg., "sawdust," 66 ♀ ♀.

WEST VIRGINIA: TUCKER COUNTY, north of Dryfork (near Harmon), Sept. 4, 1964, J.W. leg., "under boards in old sawdust, and berlese of same," 7 ♀ ♀.

Remarks.—This species is easily distinguished by the form of the spermatheca (fig. 4a, b) which shows remarkably little variation in the approximately 630 females examined. All of the specimens seen could be easily assigned by this one character alone. There are also color and facies differences which cannot be described or figured well. There are no males whatever in this sample of 630 specimens, which consists of 18 collections from eight states. The specimens were collected in five different months of the year. These data, like those for *E. lutea* and *E. frosti*, suggest that *fusca* is a parthenogenetic species, at least in the region from which it is recorded in the present study.

Several females each had a single large egg in the abdomen. Four eggs measured .28 by .16 mm., .26 by .15 mm., .26 by .17 mm., and .26 by .15 mm. The measured eggs all had the chorion well developed.

The distribution of this species in the United States differs from the pattern of the other species of *Eurygyne.* It is distributed widely in the eastern United States but it has been found outside of the immediate vicinity of the Gulf of Mexico only in sawdust piles left from sawmill activities. This pattern of distribution will be analyzed in more detail in the *Discussion* section of this paper.

Eurygyne frosti, new species. Figures 4f; 13.

Color brown; antennae, mouthparts, legs and abdomen yellowish; body covered with fine inclined yellow setae. Collar of mesothorax not extending onto humeri. Posterior margin of pronotum sinuately notched near posterior angles. Suture lateral to mesocoxae heavily ridged internally. Females with spermatheca of diagnostic form (fig. 4f). Male sex unknown.

Measurements: In slide-mounted specimens, the length from the anterior margin of the pronotum to the apex of the elytra, is about .53 mm. In dry-mounted specimens, the total length, including the retracted head and apex of abdomen, is .56–.58 mm.; the width is .30–.32 mm.

Holotype.—A female, mounted on a microscope slide, from the Archbold Biological Station, near Lake Placid, Highlands County, Florida, collected Nov. 15, 1959, by S. W. Frost, "at light." In the collection of Field Museum of Natural History.

Paratypes.—150 ♀ ♀, same data as holotype. In the collection of Field Museum of Natural History and in the S. W. Frost Collection. Numerous broken specimens not included in the type series.

Other records.—FLORIDA: BAY COUNTY, Panama City, July 10, 1965, W.S. leg., "grassy compost," 1 ♀. COLLIER COUNTY, Collier-Seminole State Park, Royal Palm Hammock, Aug. 28, 1965, W.S. leg., "litter under fern and bushes," 1 ♀; same, H.R.S. leg., "debris under banana trees," 1 ♀; 3 miles east of Monroe Station, Aug. 28, 1965, W.S. leg., "roadside grassy litter at edge of cypress swamp," 15 ♀ ♀. DADE COUNTY, Everglades National Park, Palma Vista Hammock, Aug. 27, 1965, W.S. leg., "debris at buttress of large smooth-barked tree," 1 ♀; same, H.R.S. leg., "forest floor debris, with some wood," 1 ♀. HIGHLANDS COUNTY, Archbold Biological Station, near Lake Placid, June 12, 1955, H.S.D. leg., "oak-pine leaves compost," 4 ♀ ♀; same, no microhabitat data, 1 ♀; Highlands Hammock State Park, Aug. 24, 1965, H.R.S. leg., "debris from forest floor and at buttress," 1 ♀; Aug. 23–24, 1949, H.S.D. leg., "in decaying grass pile," 4 ♀ ♀; 4 miles west of Venus, Fish Eating Creek, Aug. 25, 1965, W.S. leg., "grassy compost mixed with cypress needles," 30 ♀ ♀; H.R.S. leg., "grass mat at edge of cypress swamp," 58 ♀ ♀; same, 16 ♀ ♀; "Parker Islands," Aug. 25, 1965, W.S. leg.,

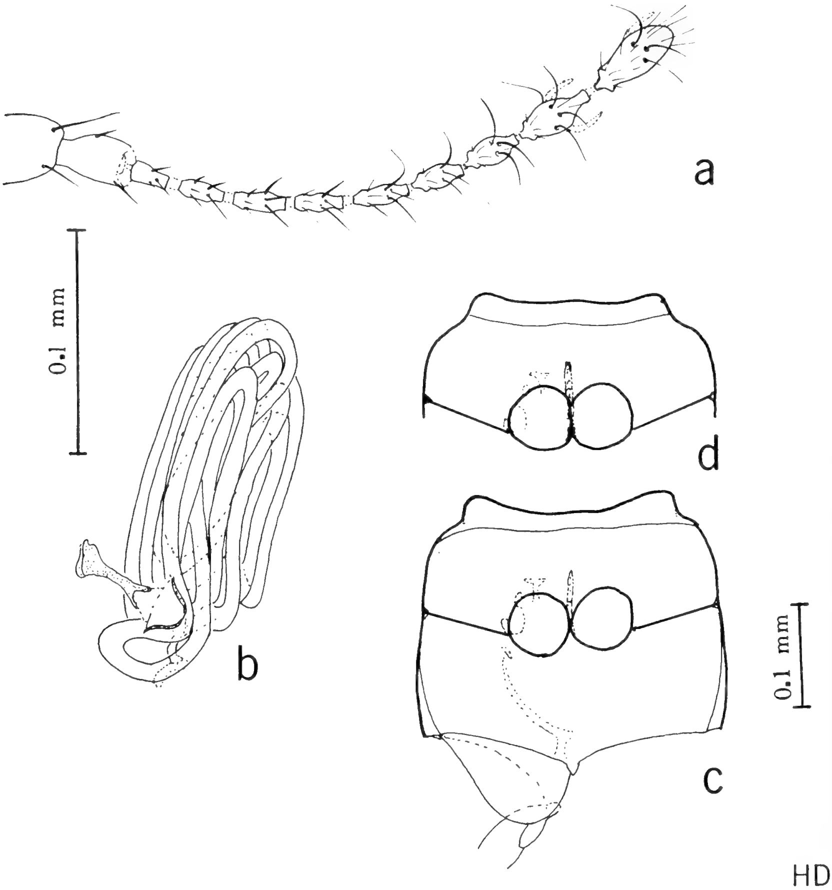


FIG. 6. *Eurygyne contorta* n. sp., *a*, antenna. *b*, spermatheca, ventral view. *c*, underside of meso- and metathorax showing collar extending onto humeri. *d*, same, of *E. intricata*, collar *not* extending onto humeri.

"litter under ferns at oak," 1 ♀; H.R.S. leg., "fern rhizome and woody debris, magnolia swamp," 1 ♀; same, but Aug. 26, 1965, 1 ♀. LEON COUNTY, south of Chaires, Aug. 29, 1965, H.R.S. leg., "sawdust pile," 1 ♀. MONROE COUNTY, 5 miles north of Flamingo, Everglades National Park, Snake Bight Trail, Aug. 27, 1965, W.S. leg., "grassy compost in sawgrass area," 6 ♀ ♀; 5 miles south of North Key Largo, Aug. 27, 1965, W.S. leg., "floor debris at log," 1 ♀. ORANGE COUNTY, Orlando, Aug. 22, 1965, W.S. leg., "grassy compost at edge of swamp," 1 ♀; "grassy compost in field," 3 ♀ ♀.

BAHAMA ISLANDS: SOUTH BIMINI ISLAND, August, 1951, C. and P. Vaurie leg., 1 ♀ (AMNH).

Remarks.—This species is dark in color, like *E. fusca*, but it is easily separated by the form of the spermatheca, which is diagnostic. Approximately 370 females (including fragmentary individuals) have been studied on permanent or temporary slide preparations. The spermatheca, though more variable than in *lutea* and *fusca*, is diagnostic and no variations were seen that created problems of identification. Eight females each had a single egg which averaged .32 by .17 mm. In 13 specimens, the apical group of wing hairs ranged from 53 to 63 and averaged 57, the same as in *lutea*.

The 23 collections are from seven counties in Florida and from the Bahama Islands and span a period of six months of the year, yet all of the approximately 370 specimens collected are females. Again, as in *E. lutea* and *E. fusca*, the evidence points to complete parthenogenesis in these populations.

The mouth-parts of the type series appear seemingly aberrant; the palpiger of the labial palpi appears different from that of the other collections of *frosti*, and the lacinia and galea seem to be absent in the type specimens. In addition, the stipes is angled mesad. I have interpreted these differences as artifacts of preservation and preparation. The type lot was collected "at light" and had been dried (and perhaps subjected to other treatment as well) before being returned to alcohol. Whatever the treatment, the natural elasticity of the exoskeleton was not restored when the specimens were processed for microscope slide mounts. In these seemingly aberrant mouth-parts, the galea is hinged inward (dorsad) into the head capsule, and is not visible, the lacinia is similarly out of view in most specimens, and the labial palps are directed dorsad from the hinge line at the anterior margin of the mentum, thereby showing a different angle of the palpigers and an apparently different form. When two specimens of *frosti* still in alcohol were dissected, the "missing" galea and lacinia were found tucked behind the mentum and labial palpi, the galea being folded on itself as well.

The largest collection was made "at light" at the Archbold Biological Station. This raises a problem of interpretation since Ptiliidae, as stated earlier in this paper, have not been regarded as possessing well-developed powers of directional flight. When only a few specimens are encountered on a light sheet or in a light trap, one can assume that Ptiliidae that are dispersing passively have been intercepted by the light sheet or trap. The type lot of *frosti*, however,

consists of more than 200 specimens taken "at light" in a single night. Frost (1963) states that the Ptiliidae (=Trichopterygidae) came to the lights at the Archbold Biological Station early when the light traps were operated between 5:30 and 6:00 PM on Nov. 10–16, 1960. "No counts were made of the Trichopterygidae, but observations revealed that they came decidedly before 6 PM, usually within a few minutes and sometimes in enormous numbers, striking against the baffles of the trap like buckshot." If these actually represented an intercepted sample of passively floating Ptiliidae, there must have been astonishing numbers floating in the air. The "at light" sample submitted by Dr. Frost contained four species of *Eurygyne,* of which *frosti* accounted for most of the collection.

Eurygyne suteri, new species. Figures 7a, b; 13.

Color light brown, antennae and mouth parts yellow; body covered with fine recumbent yellow setae. Collar of mesothorax not extending onto humeri. Suture lateral to the mesocoxae marked for its full length by a heavy internal skeletal ridge. Females with spermatheca of diagnostic form (fig. 7a, b). Male sex unknown.

Measurements: In slide-mounted specimens, the length from the anterior margin of the pronotum to the apex of the elytra is about .54 mm.; the width is about .32 mm.

Holotype.—A female, mounted on a microscope slide, from Palma Vista Hammock, Everglades National Park, Dade County, Florida, collected August 27, 1965, by Walter Suter, from berlese sample of floor litter in buttress of large smooth-barked tree. In the collection of Field Museum of Natural History.

Paratypes.—Same data as holotype, 5 ♀ ♀ (1 callow); "litter in small, limestone sink," 3 ♀ ♀; "floor litter on slope from road into swamp," 5 ♀ ♀; no microhabitat data, 8 ♀ ♀ (1 callow); same data but H. R. Steeves, Jr. leg., "pockets of forest floor debris, some with wood," 1 ♀; "forest floor debris at fallen logs," 2 ♀ ♀. COLLIER COUNTY, 3 miles east of Monroe Station, Aug. 28, 1965, H. R. Steeves, Jr. leg., "hammock-like swamp grass litter," 1 ♀; same data except "roadside grassy litter at edge of swamp," 5 ♀ ♀. DADE COUNTY, Florida City, Aug. 26, 1965, W. Suter leg., "no microhabitat data," 1 ♀. HIGHLANDS COUNTY, 4.5 miles west of Venus, at Fish Eating Creek, Aug. 25, 1965, H. R. Steeves, Jr. leg., "grass mat at edge of cypress swamp," 7 ♀ ♀; same locality, W. Suter leg., "grassy compost mixed with cypress needles near water," 2 ♀ ♀. ORANGE COUNTY, Orlando, Aug. 22, 1965, "grassy compost at edge of swamp," 1 ♀; "litter at pine buttress," W. Suter leg., 1 ♀ (callow).

Remarks.—This species is similar to *E. frosti*, but is lighter in color. It is easily separated from all the other species by the diagnostic form of the spermatheca. The 46 specimens examined, from 15 collections, were all females; no males have been found. The sample

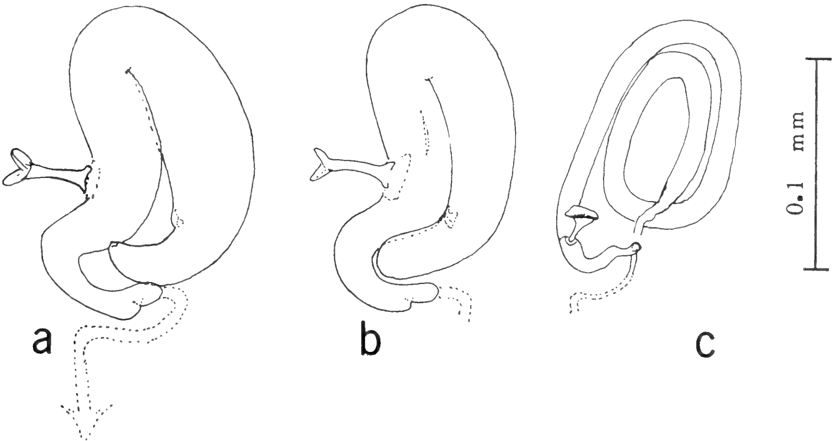


FIG. 7. *a*, *Eurygyne suteri* n. sp., spermatheca, ventral view. *b*, same, another individual, showing variation. *c*, *Eurygyne steevesi* n. sp., spermatheca, ventral view.

is not large but, in view of the pattern of parthenogenesis within the genus, it is likely that *E. suteri* is also a completely parthenogenetic species, at least in the range here recorded. One female had a single, relatively huge egg in the abdomen that measured .32 by .20 mm., or half the length of the animal. In 20 females, the apical group of wing hairs ranged from 57 to 64 with a mean of 61.

Eurygyne suteri Dybas was invariably collected in the field with the far more abundant *lutea*. The 15 berlese samples in which the 46 specimens of *suteri* were found also contained 2,815 female specimens of *lutea*, 190 female *frosti* (8 lots), 114 female *contorta* (4 lots), 15 specimens of *wagneri* (2 lots), and one female of *steevesi*. Thus, it is an extremely minor component of the *Eurygyne* fauna of the United States, at least in the microhabitats sampled so far.

Eurygyne steevesi, new species. Figures 7c; 13.

Color brown, collar of mesothorax not extending onto mesopleural humeri. The suture lateral to the mesocoxae, not marked with a heavy internal skeletal ridge except near coxa. Female spermatheca of diagnostic form, as shown in Figure 7c. Male sex unknown.

Measurements: In slide-mounted specimens, the length from the anterior margin of the pronotum to the apex of the elytra is .51 mm.; the width of the pronotum is .32 mm.

Holotype.—A female, mounted on a microscope slide, from Florida City, Dade County, Florida, collected Aug. 26, 1965, by Walter Suter, in debris under banana. In the collection of Field Museum of Natural History.

Paratypes.—Same data as type, 1 ♀; DADE COUNTY, Everglades National Park, Palma Vista Hammock, Aug. 27, 1965, H. R. Steeves, Jr. leg., "forest floor debris at fallen logs," 1 ♀.

Other record.—HIGHLANDS COUNTY, Archbold Biological Station, near Lake Placid, Nov. 15, 1959, S. W. Frost leg., "at light" (specimen later lost), 1 ♀.

Remarks.—This species is easily distinguished by the diagnostic form of the spermatheca. It also differs from all the species described in this paper in the condition of the suture lateral to the mesocoxae, which is marked internally by a heavy endoskeletal ridge only near the coxa; laterally it is a fine surface suture. Since only four females have been seen, it is not possible to say at present whether the species is parthenogenetic or not. In one specimen, the number of wing hairs in the apical group is 56 in one wing and 53 in the other.

Eurygyne wagneri, new species. Figures 5a–d; 13.

Color yellow-brown. Collar of mesothorax extending onto mesopleural humeri (fig. 6c). Middle antennal segments short, as in figure 5a. The suture lateral to the mesocoxae marked internally by a heavy endoskeletal ridge. Spermatheca of female as in figure 5b, c. Male aedeagus as in figure 5d. Male with a median fovea on front of head.

Measurements: Length from anterior margin of pronotum to apex of elytra: in males, .45–.50 mm.; in females, .48–.51 mm.; width of pronotum: .27–.29 mm.

Holotype.—A female, mounted on a microscope slide, from Florida City, Dade County, Florida, collected Aug. 26, 1965, by Walter Suter, "debris under banana," in pine-palmetto woods. In the collection of Field Museum of Natural History.

Allotype.—A male, mounted on a microscope slide, same data as the holotype. In the collection of Field Museum of Natural History.

Paratypes.—Same data as the holotype, 24 ♀ ♀, 16 ♂ ♂; same, but no microhabitat data, 4 ♀ ♀, 10 ♂ ♂. Everglades National Park, Palma Vista Hammock, Nov. 26, 1961, J. Wagner leg., "floor duff," 2 ♀ ♀, 1 ♂; same locality, Aug. 27, 1965, W. Suter leg., no microhabitat data, 1 ♀.

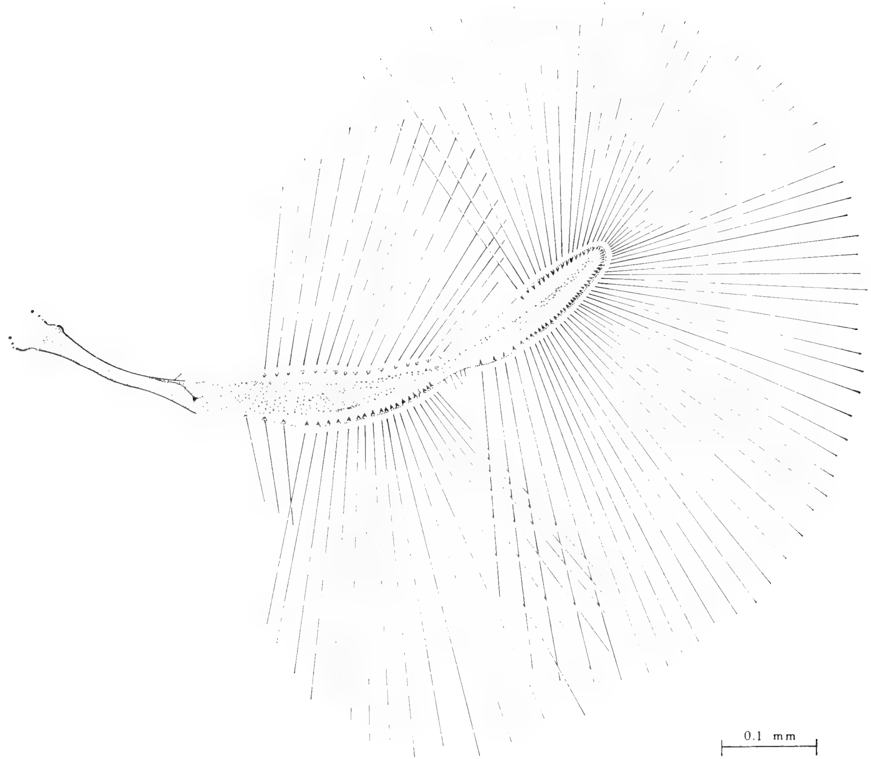


FIG. 8. *Eurygyne lutea* n. sp., metathoracic wing (description in text).

Remarks.—This species is related to *Eurygyne contorta* in the form of the mesothoracic collar, the delimiting line of which extends onto the mesopleural humeri, as in Figure 6c. The females differ from *contorta* by the pale color, and from it and all the other species described in this paper by the shorter antennal segments (fig. 5a), and the shape of the spermatheca. The males can be separated from the only other males known so far, those of *intricata,* by the condition of the mesothoracic collar, the short antennal segments, and the presence of a fovea on the frons.

One of the females had a single large egg in the abdomen that measured .33 by .22 mm. In 43 specimens (21 ♂♂, 22 ♀♀), the wing hairs in the apical group ranged from 36–49, with a mean of 44. There was no significant variation between the sexes in the wing hairs.

Eurygyne wagneri is the only species on the mainland of the United States in which the male sex is known. The sex ratio in the 60 specimens known is 33 ♀♀ : 27 ♂♂.

Eurygyne contorta, new species. Figures 6a–c; 13.

Color brown, shining; antennae, legs, and underside of abdomen lighter; sparsely covered with light-colored, inclined hairs. Body elongate-oval and somewhat flattened in form. Collar of mesothorax, extending onto mesopleural humeri (fig. 6c). Suture lateral to mesocoxae marked internally by a heavy endoskeletal ridge. Antennae as in Figure 6a. Spermatheca (fig. 6b) more convoluted than in the related *wagneri.* Male sex unknown.

Measurements: Length of slide-mounted specimens from anterior margin to apex of the elytra, .51 mm.; width, .28 mm.

Holotype.—A female on a microscope slide, from Fish Eating Creek, 4 miles west of Venus, Highlands County, Florida, collected Aug. 25, 1965, by Walter Suter, "cypress swamp, in grassy compost mixed with cypress needles near water." In the collection of Field Museum of Natural History.

Paratypes.—Same data as holotype, 21 ♀♀; same, H. R. Steeves, Jr. leg., "cypress swamp, grass mat at edge," 99 ♀♀.

Other records.—FLORIDA: COLLIER COUNTY, east of Ochopee, June 17, 1965, W.S. leg., "cypress buttress in cypress-palmetto-maple swamp along U. S. highway No. 41," 1 ♀. DADE COUNTY, Everglades National Park, Palma Vista Hammock, Aug. 27, 1965, H.R.S. leg., "forest floor debris at fallen logs," 1 ♀. HIGHLANDS COUNTY, Archbold Biological Station, near Lake Placid, Nov. 15, 1959, S. W. Frost leg., "at light," 1 ♀; same, June 19, 1965, W.S. leg., "pine buttress in pine-palmetto stand," 2 ♀♀; "Parker Islands," Aug. 25, 1965,

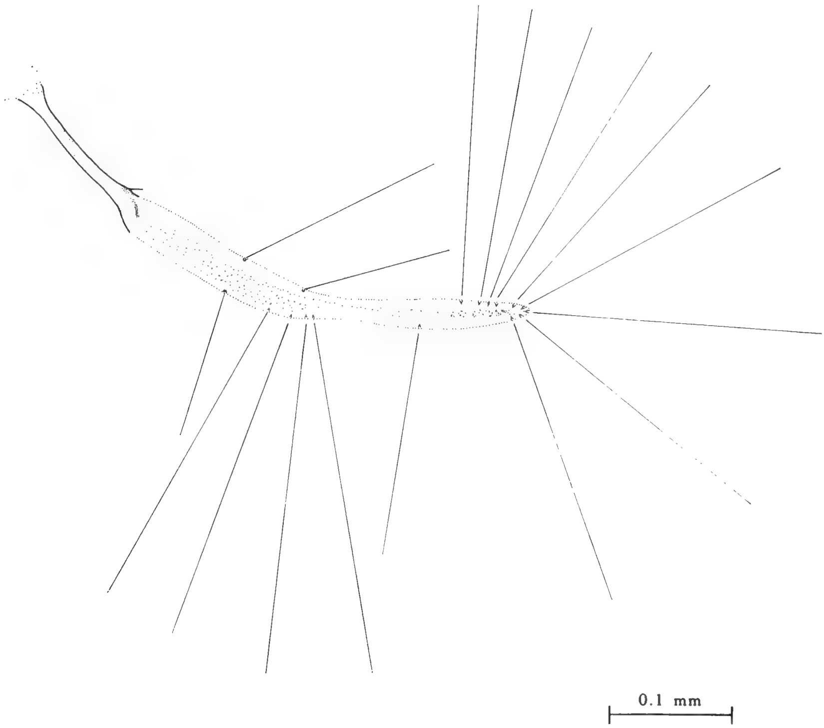


FIG. 9. *Eurygyne intricata* n. sp., metathoracic wing, showing a reduced stage of marginal hairs in a polymorphic population.

W.S. leg., pine-oak grove, "litter under ferns," 1 ♀; "litter at log," 1 ♀; H.R.S. leg., "forest floor debris," 1 ♀; Highlands Hammock State Park, Aug. 24, 1965, H.R.S. leg., "forest floor debris, and at buttress," 9 ♀ ♀. SEMINOLE COUNTY, 2 miles north of Longwood, Aug. 23, 1965, H.R.S. leg., pine-oak-palmetto forest, "debris from palmetto under rotten log," 1 ♀; 3 miles north of Longwood, W.S. leg., "oak-palmetto pseudofork," 2 ♀ ♀; VOLUSIA COUNTY, 2 miles southwest of Enterprise, Aug. 23, 1965, H.R.S. leg., "oak log," 1 ♀.

Remarks.—This species is more elongate and more flattened in form than the members of the *intricata* group. It is most closely related to *wagneri* in the condition of the collar of the mesothorax, but differs in the form of the spermatheca and the proportions of the antennal segments. Four females each had a single egg that averaged .32 by .20 mm. In 22 females, the apical group of marginal wing hairs ranged from 56–62, with a mean of 60.

All of the 142 specimens are females; no males are known. Since these represent 13 collections made over a span of six months in five counties in Florida, it is very probable that *contorta*, too, is a completely parthenogenetic species, like most of the *Eurygyne* species described in this paper.

Discussion

Though no species of *Eurygyne* have been previously recorded from the United States, the genus is clearly a dominant group of featherwing beetles in the floor stratum of Florida. To illustrate this, I have tabulated comparable collections made in the summer of 1965 in 30 counties that span the whole state of Florida. The collections were all made by the same person, Dr. Walter Suter of Carthage College, and total 12,151 Ptiliidae representing at least ten genera. Parenthetically, this is probably the finest sample of Ptiliidae of the floor stratum of a geographic area ever made. Of this total, the specimens of *Eurygyne* number 5,723, or 47%.

If, on the other hand, the percentages are calculated separately for northern versus peninsular Florida, a significant difference appears. I have selected a more or less arbitrary dividing line roughly at the point of greatest constriction near the base of the peninsula (fig. 14). For convenience, the three counties (Levy, Marion, and Volusia) dissected by this line are assigned to peninsular Florida. South of this line, in peninsular Florida, there are 8,075 Ptiliidae from 13 counties in the sample. The *Eurygyne* number 4,975 specimens, or 62%. North of this line there are collections from 17 Florida counties, totalling 4,076 Ptiliidae, of which 748, or 18%, are *Eurygyne*. Thus, there is a striking drop in the proportion of *Eurygyne* as one leaves peninsular Florida. The same pattern appears in the number of species of *Eurygyne*—all seven known U. S. species occur in peninsular Florida, but only three of these have been collected outside this area in the United States. These facts merely reflect, I believe, the essentially tropical distribution of the genus *Eurygyne*.

Parthenogenesis has not been reported before in the Ptiliidae, but the evidence presented in this paper strongly supports its occurrence in five species of *Eurygyne*. These species are *frosti, lutea, fusca, contorta,* and *suteri,* of which I have examined 370, 2,500, 630, 142, and 46 females, respectively, without seeing a single male. Males are known for only two of the eight species described in this paper. One of these is *wagneri* from Florida, which has a roughly even sex ratio

in the 60 specimens known; the other is *intricata* from South Bimini Island off the coast of Florida, which has a sex ratio of 43% males and 57% females in the 581 specimens that were sexed. The last new species, *steevesi,* is only known from three collections totalling four females, so judgment must be suspended as to its condition. Thus, of the eight new species described in this paper, two are definitely bisexual, five appear to be parthenogenetic, and the condition of one is uncertain.

Not all the evidence, though, is consistent with the hypothesis of complete parthenogenesis in *Eurygyne.* A spermatheca is a nonfunctional structure in a completely parthenogenetic species. Such nonfunctional structures ought to become vestigial in time, or, at least, ought to become more variable because of less stringent selection. Yet all the presumptively parthenogenetic species retain the spermatheca in apparently functional form and, moreover, exhibit little variability in this structure.

Alternative hypotheses to that of complete parthenogenesis, are that males are produced only at certain times of the year, or that they have unusual habits which would prevent their being collected with the females, but such sexual differences are unknown in any Ptiliidae. Another possibility is that we may be sampling peripheral parthenogenetic populations of species which have males in one part of the range and not in another, in which case the species as a whole is not completely parthenogenetic. Suomalainen (1962), in a recent review of parthenogenesis in insects, cites several cases in which a given species is bisexual in one area and parthenogenetic in another. The weevil genus *Otiorrhynchus,* for example, has at least ten species of this kind in Europe. In most of these, the bisexual races occur outside the areas covered by ice during the Würm glaciation, while the parthenogenetic races have, for the most part, spread into the areas later freed from ice. Suomalainen suggests possible reasons for these different distributions in the parthenogenetic and bisexual races in *Otiorrhynchus.* A somewhat similar case has been presented by Reichle (in press) on a species of beetle of the family Pselaphidae (*Bythinopsis tychoides* Brendel) that is found in bogs in northeastern United States. There is a roughly equal sex ratio in New York and New Jersey; whereas west of the Allegheny Mountains, only females have been collected.

The range of *Eurygyne,* on the basis of unpublished data as well as on the localities recorded in this paper, is primarily tropical. Its northern extension into the United States may well be a peripheral

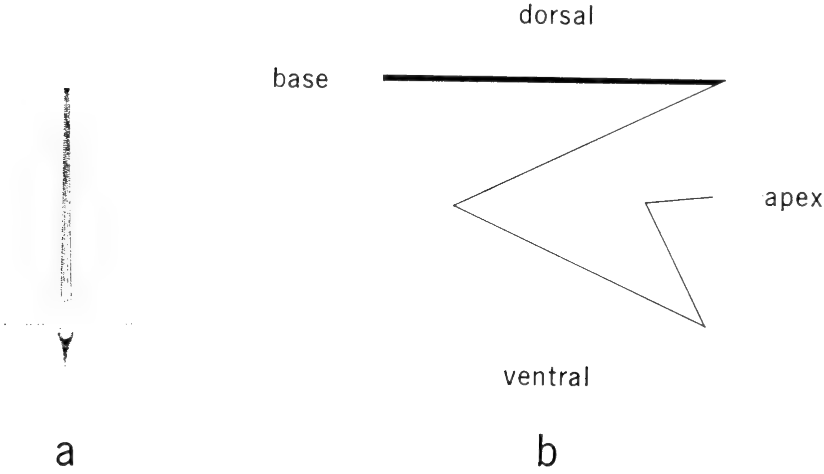


FIG. 10. *Eurygyne lutea* n. sp., *a*, portion of a marginal wing hair, showing transparent, flexible basal portion, and insertion in socket in wing membrane. *b*, diagram of wing-folding pattern. In the terminology of Forbes (1926) the transverse folds are convex—concave—concave—convex.

one, and the main ranges of the species treated here may be in the West Indies or in Middle and South America where the genus has not yet been studied. When the more tropical components of *Eurygyne* are studied, the pattern of parthenogenesis may appear to be different.

Returning to the problem of the 'non-functional' spermatheca, a simple explanation for its uniformity, in view of relaxed selection, suggests itself. The two main sources of genotypic variation in bisexual species are gene flow and recombination (see Mayr, 1963, for a recent review). In a completely parthenogenetic species, gene flow is precluded and recombination of genes is no longer possible, at least between different individuals. Segregation within an individual may be possible depending on whether the parthenogenesis is of the meiotic or ameiotic type (White, 1954). In any case, mutation is left as a main immediate source of genotypic variability in a completely parthenogenetic form. In such a species, the accumulation of viable mutations in the loci affecting the form and structure of the spermatheca may be so slow as to have little effect on its variability over long periods of time. This alone may account for the retention of an apparently functional spermatheca, and its low variability in the presumptively parthenogenetic species of *Eurygyne*.

Nothing is known, of course, of the cytogenetics of *Eurygyne*, but in the *Otiorrhynchus* weevils, all of the parthenogenetic species stud-

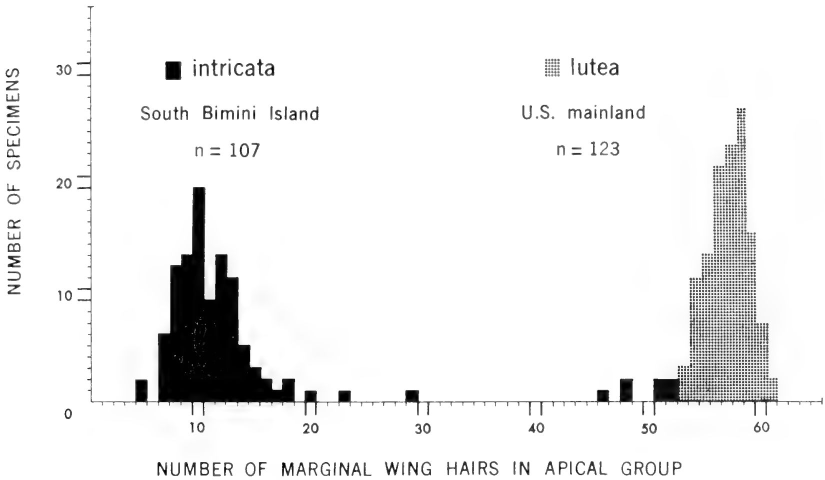


FIG. 11. Graph of number of marginal wing hairs in apical group in *Eurygyne intricata* n. sp. and *lutea* n. sp.

ied to date are polyploid. In those cases, as stated by Suomalainen (1962), "the newly arisen mutations have difficulty expressing themselves, as they are counterbalanced by several doses of the original allele."

Because recombination of genes between different individuals is no longer possible in parthenogenetic forms, their genetic systems are presumably at a disadvantage in the long run because of the lack of adaptability to changing circumstances. In the short run, though, a completely parthenogenetic species may be quite successful. Most of the parthenogenetic *Otiorrhynchus* weevils have larger ranges than their bisexual relatives (Suomalainen, 1962), though here the factor of polyploidy is also involved.

The advantages of parthenogenesis (White, 1954, and Suomalainen, 1962) include these: 1) parthenogenesis permits the fixation of genotypes particularly favorable for special situations; 2) it facilitates expansion into new areas because any individual at any stage of development can establish a population in a favorable place; 3) it increases fecundity by a factor of two because all of the eggs can produce females—none are 'wasted' (Mayr, 1963) on males. There are also some other possible genetic advantages (Dobzhansky, 1951).

All of these advantages may apply to the parthenogenetic species of *Eurygyne;* but the third point, the increase in fecundity, seems particularly relevant. Earlier, it was shown that only one relatively huge

egg is matured in the abdomen at one time. This is true of the two bisexual species, *E. intricata* and *wagneri*, as well as of five parthenogenetic species, *E. lutea, fusca, frosti, contorta*, and *suteri*, so it very probably holds throughout the entire genus. These mature eggs are approximately one-half the total length of the entire body! In some other unrelated genera in the Ptiliidae (e.g., five genera of U. S. Pterycini, unpublished data), there is similarly only one large mature egg at a time, indicating that this habit may be widespread in the family. The Ptiliidae have active staphyliniform larvae (Hinton, 1941, and unpublished data) and their eggs must be provided with enough yolk for embryogenesis to continue until the highly organized larva is fully formed and self-sufficient. Presumably, this explains why there must be such a relatively large egg in such a small insect. Rensch (1948) has pointed out that one of the consequences of evolution toward small size in arthropods is a reduction in the number of eggs that can be accommodated and matured in the abdomen, because each egg must be furnished with sufficient yolk to complete embryogenesis; in the extreme case there is room for only one egg. Rensch regards egg number and egg size as important factors in setting lower limits to the evolution of small size in arthropods.

There are no data on how long a female featherwing beetle may live and reproduce nor on how long it takes a single egg to mature. It would seem, though, that a low average fecundity per female must be postulated. This is difficult to reconcile with the high densities of Ptiliidae encountered in some temporary microhabitats, and with the passive dispersal suggested by the structure of the metathoracic wings, a method of dispersal that implies considerable wastage of individuals. When more is known about these little animals, the apparent discrepancies in these statements may be reconciled. For one thing, there may have been a compensating increase in the rate of development as evolution progressed toward small size and fewer eggs. Unfortunately, there is almost no information on rates of development in the Ptiliidae. The only data in the literature (Hinton, 1941) suggest a period of development of three weeks from egg to adult in *Acrotrichis fascicularis* (Herbst) which is only remotely related to *Eurygyne*. Featherwing beetles seem to reproduce continuously rather than seasonally, judging by the presence of larvae and callow adults at different periods of the year. Thus, the 'innate capacity for increase' (Andrewartha and Birch, 1954) may well be substantially greater than the minimal egg number implies.

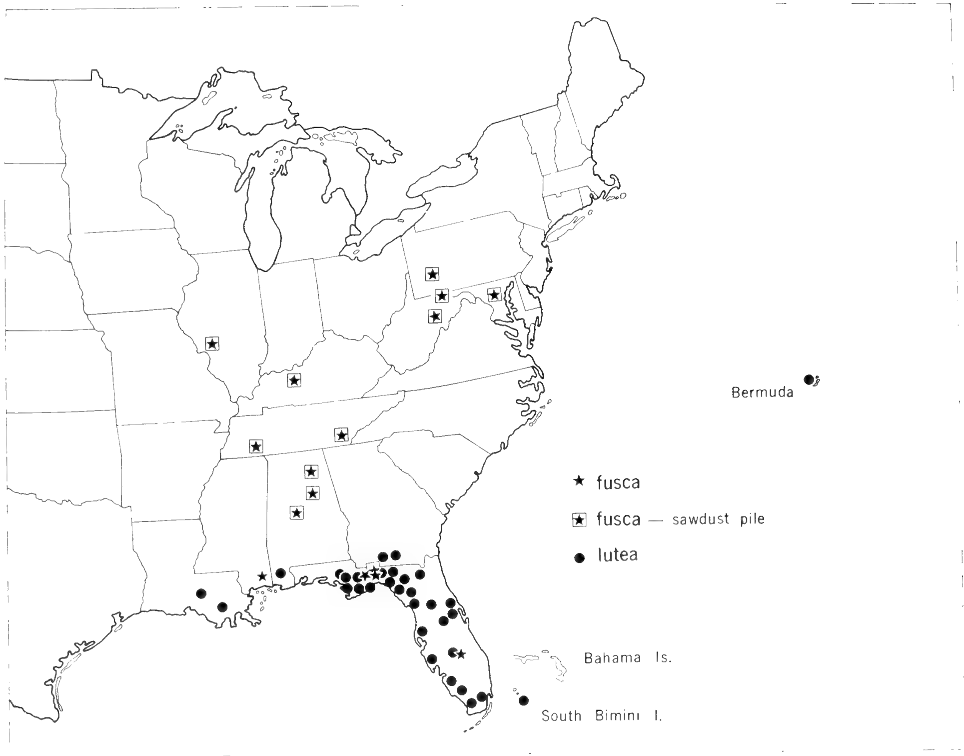


FIG. 12. Distribution map of *Eurygyne lutea* n. sp. and *fusca* n. sp. Each symbol may represent one or several collections within a county or parish.

In any case, the sudden doubling of a critically low fecundity through parthenogenesis, may confer a large selective advantage on a clone imbedded in a biparental population—a very large advantage, even when compared with the magnitudes of selective pressures now being discovered in natural populations (Ford, 1964). Though this may be of short-range evolutionary advantage, it does not preclude the temporary success of parthenogenetic populations in those insects, with appropriate genetic potentialities. If, indeed, increased fecundity is a major advantage of parthenogenesis, there should be a higher incidence of parthenogenesis in groups where evolution toward small size has greatly reduced the number of eggs produced. The Ptiliidae, on these grounds, ought to provide a test of this prediction once they are better known. As mentioned earlier, the genus *Eurygyne* will probably have many more species throughout its pantropical range when studied with appropriate techniques. In connection with general problems of parthenogenesis and evolution, there is obviously an advantage in studying a genus that has numbers of both kinds of species. Patterns with respect to geographic range, microhabitats, variation, numbers, and other population aspects may become evident when enough parthenogenetic and bisexual species within a single genus are studied and compared.

There is a further point. With one exception, the genus *Eurygyne* in the United States, according to present records, is restricted to Florida and to the southern portions of the Gulf states of Louisiana, Mississippi, and Alabama (figs. 12, 13). The northern limit is essentially defined by the winter isotherm of 50° F. The exception to this pattern is *fusca*, most of whose records are from sawdust piles left from sawmill activities north of this line; none is from a 'natural' microhabitat. South of this line, however, in addition to records from sawdust piles (Leon and Jefferson counties in northern Florida), there are small collections from "oak-pine leaves compost," "at light," and "sifting floor-litter in mixed pine-deciduous forest." These are preliminary data and much more sampling needs to be done before definitive conclusions can be drawn; nevertheless, they form a consistent pattern. The genus is clearly tropical and subtropical and, in the United States, its distribution is centered in Florida where all seven U. S. species occur. Only two species are recorded from outside the state of Florida; one of these, *lutea*, is restricted in the United States to the vicinity of the Gulf of Mexico. The evidence, then, suggests that the parthenogenetic species *fusca* is able to extend its range outside the main *Eurygyne* range into 'artificial' microhabitats provided

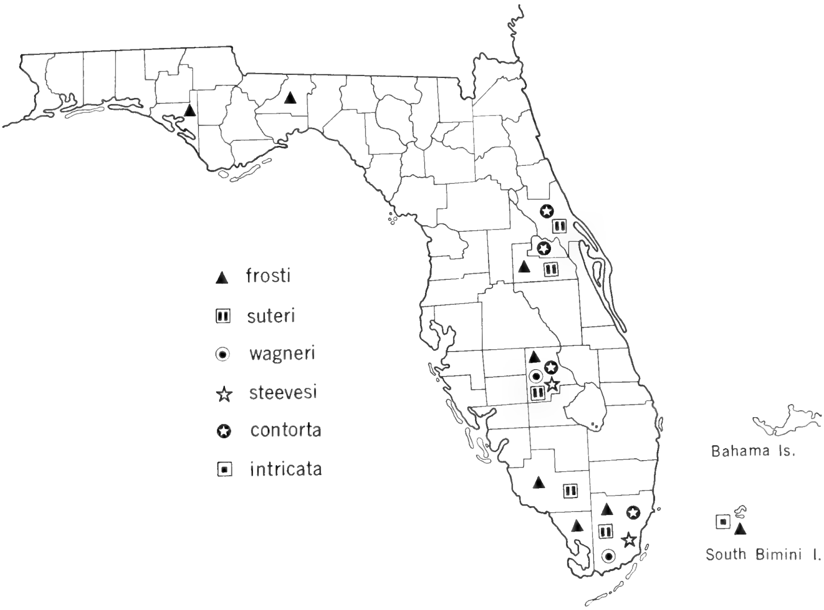


FIG. 13. Distribution map of *Eurygyne* species. Each symbol may represent one or several collections within a county or island. None of the species plotted is presently known to occur outside the area shown in the map.

by sawdust piles in the woods. Perhaps its spread into these situations is facilitated by its parthenogenesis; any individual encountering a favorable sawdust pile can establish a population.

Sawdust piles, it can be assumed, provide a warm, buffered environment that is relatively stable over long periods of time. Oxidation provides heat which is dissipated slowly through the well-insulated mass; a large pile is quite hot in the center. It may require five to ten years for a sawdust pile to acquire an appreciable micro-fauna, which may then persist for a number of years, perhaps up to twenty (Suter, personal communication). At present it is still not possible to say from which microhabitat of the forest floor, or its extensions, most of the sawdust pile fauna is derived. *Eurygyne fusca* is known from a few collections made in forest-floor litter but most of the records are from sawdust piles.

A new sawdust pile is a kind of sweepstakes situation, as suggested in conversation by my colleague Dr. Monte Lloyd. The chances of a given female finding a suitable pile are extremely small, true, but once the pile is found, the ecological opportunity for a rapidly expanding

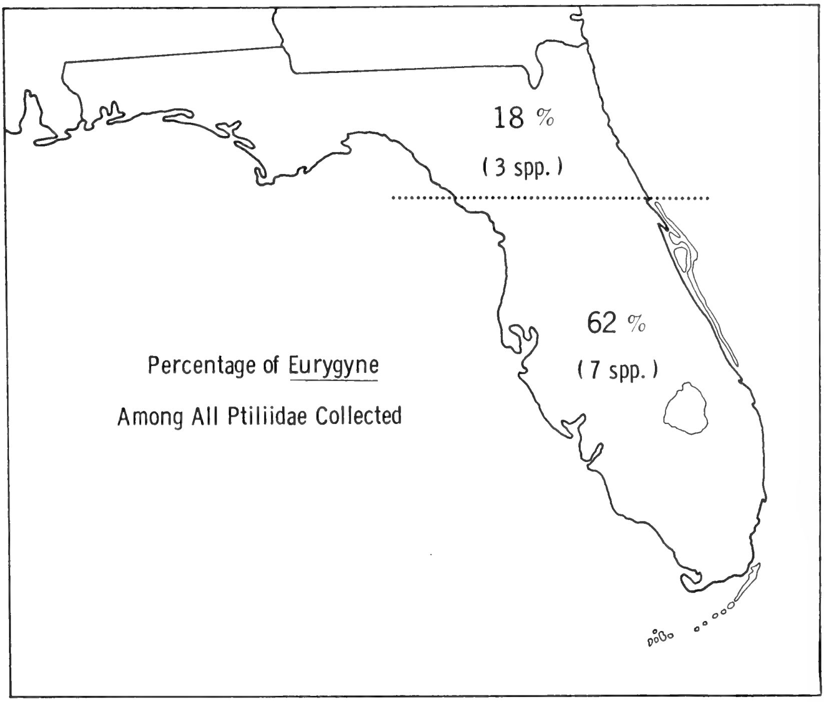


FIG. 14. Percentage of specimens of *Eurygyne* in comparable collections of Ptiliidae from the floor stratum in northern Florida, as contrasted with peninsular Florida. The collections were all made by one person (Walter Suter) in one summer (June to August, 1965). The northern collections total 4,076 Ptiliidae from 17 counties, and the peninsular collections total 8,075 Ptiliidae from 13 counties. There is a marked drop in the percentage of specimens of *Eurygyne* in the collections of Ptiliidae in northern Florida, and a similar drop in the number of species represented.

population is great, especially for a parthenogenetic species like *fusca*. Moreover, a large sawdust pile probably provides a favorable, stable environment, in one part or another, over a period of many years; the sawdust pile at the type locality near Fieldon, Illinois, still contained *fusca* after six years in 1965, and one dispersing female was collected floating in the air above the pile. Sawdust piles seem to have relatively few species of beetles, mostly in the families Ptiliidae, Pselaphidae, Scydmaenidae, Histeridae, and Staphylinidae, but these are characteristically present in large numbers (Suter, Wenzel, Wagner, personal communications). There may be further genetic advantages to parthenogenesis in such large populations established by single founders. A closely inbreeding bisexual population, derived from a

single fertilized female, provides the conditions for increasing homozygosity and the expression of deleterious recessives, and may thus result in a lower level of fitness of the population.

A similar pattern of a southern insect maintaining itself in favorable microhabitats in northern localities—again in sawdust piles—is seen in *Zorotypus hubbardi* (order Zoraptera). The distribution of this species has been worked out in detail by Gurney (1959), Riegel and Ferguson (1960), and Riegel (1963). In the southern states of Florida, Mississippi, Louisiana, and South Carolina, this species occurs under the bark of stumps and in logs; but in most of its recorded range, which extends north to Delaware and Pennsylvania in the east, and Iowa, Kansas, and Oklahoma to the west (see map in Riegel, 1963), it occurs almost exclusively in sawdust piles. For example, of 34 collections in eight states outside the Gulf states region, all but one were from sawdust piles (Riegel and Ferguson, 1960), and Riegel (1963) believes that the species can maintain itself in the north only by chance colonizations of temporarily favorable sawdust heaps.

Finally, it has been shown that *Eurygyne intricata*, in contrast to all the other species described in this paper, is strongly polymorphic with respect to the number of marginal hairs of the metathoracic wings (figs. 9, 11). Since the marginal hairs account for much the greater part of the expanse of the wing, it is highly probable that the individuals with great reduction in marginal hairs are unable to use their wings for passive dispersal. Of 107 specimens of *intricata* studied, 7 or 6½% had a full complement of marginal hairs (an average of 50 in the apical group) while the rest showed an extreme but variable degree of reduction. This suggests a balanced polymorphism resulting from conflicting selective forces (for recent reviews see Mayr, 1963, and Ford, 1964). The polymorphic population of *intricata* was collected on South Bimini Island in the Bahamas. The island is only 4 by 1¾ miles in extent, has a low relief, and is subjected to prevailing southeast breezes during the summer when the collections were made (Vaurie, 1952). Under these circumstances there is probably strong selection against fully-winged individuals because of the hazard of being wafted out to sea and lost.[1] On the other hand, there is undoubtedly need for dispersal between habitats on the island and between islands from time to time, hence selection

[1] Since this was written, a comparable situation in wind-dispersed seeds has been reported by Carlquist (1966). In the seeds of certain mainland Compositae, the pappus is well developed and functions for aerial flotation, while in related Pacific island species, the pappus is greatly reduced, with correspondingly diminished powers of dispersal.

for some fully-winged individuals in the population. When other populations of *intricata* are discovered, it will be of interest to compare the degree of polymorphism of the wings with reference to the habitat.

Acknowledgements

I am indebted to many individuals and institutions for specimens and for help of various kinds. Among these are the Archbold Biological Station, Lake Placid, Florida, in the persons of Richard Archbold and L. J. Brass; the American Museum of Natural History, particularly Mrs. Patricia Vaurie, Dr. Jerome G. Rozen, Jr., and Dr. Mont Cazier (present address: Arizona State University) and the Illinois Natural History Survey (Drs. H. H. Ross and L. Stannard). Dr. S. W. Frost, The Pennsylvania State University; Dr. John Wagner, Kendall College; Dr. Orlando Park and Stewart Peck, Northwestern University; and Dr. Floyd Werner, University of Arizona, have provided many specimens. Harrison R. Steeves, Jr., Birmingham, Alabama, has provided rich collections of *Eurygyne* from southern Florida. Above all, I am indebted to Dr. Walter Suter, Carthage College. He has systematically and carefully sampled the microhabitats of the floor stratum and its extensions in many parts of the United States over the years, and his collections form the major part of the material upon which this study is based.

Dr. Robert Inger of Field Museum of Natural History and Dr. Monte Lloyd, University of California (Los Angeles) have critically reviewed parts of the paper and discussed the ideas with me. My colleague, Dr. Rupert Wenzel has read the paper and contributed a number of helpful suggestions. Mrs. Gail Dittmer has also read the paper carefully and helped in many ways. I owe especial thanks to Mr. Christian Y. Oseto for technical aid of various kinds, including microscope slide preparations and preparation of the distribution maps and several of the illustrations.

Finally, I wish to gratefully acknowledge the help of the National Science Foundation (Grant GB-2697) with whose financial support much of the work was accomplished.

REFERENCES

Andrewartha, H. G. and L. C. Birch
1954. The Distribution and Abundance of Animals. Univ. Chicago Press. xv+782 pp.

BARBER, H. S.

1924. New Ptiliidae Related to the Smallest Known Beetles. Proc. Ent. Soc. Wash., **26**, pp. 167–178, 2 pls.

BRITTEN, H.

1926. Coleoptera, Ptiliidae (Trichopterygidae). Trans. Linn. Soc., London (2), **19**, pp. 87–92.

CARLQUIST, SHERWIN

1966. The Biota of Long Distance Dispersal. II. Loss of Dispersability in Pacific Compositae. Evolution, **20**, pp. 30–48.

DOBZHANSKY, T.

1951. Genetics and the Origin of Species (3rd ed.). Columbia Univ. Press, x+364 pp.

DYBAS, H. S.

1961. A New Fossil Feather-wing Beetle from Baltic Amber (Coleoptera: Ptiliidae). Fieldiana, Zool., **44**, pp. 1–9, 5 figs.

FORBES, W. T. M.

1926. The Wing Folding Patterns of the Coleoptera. Jour. N. Y. Ent. Soc., **34**, pp. 42–68, 91–139.

FORD, E. B.

1964. Ecological Genetics. Methuen, London; J. Wiley, New York, xv+335 pp.

FROST, S. W.

1962. Winter Insect Light-trapping at the Archbold Biological Station, Florida. The Florida Entomologist, **45**, pp. 175–190.

1963. Ibid. **46**, pp. 23–43.

GURNEY, A. B.

1959. New Distribution Records for *Zorotypus hubbardi* Caudell. (Zoraptera), Proc. Ent. Soc. Wash., **61**, pp. 183–184.

HINTON, H. E.

1941. The Immature Stages of *Acrotrichis fascicularis* (Herbst) (Col., Ptiliidae), Ent. Monthly Mag., **77**, pp. 245–250.

HORRIDGE, G. A.

1956. The Flight of Very Small Insects. Nature, **178**, pp. 1334–1335.

MATTHEWS, REV. A.

1872. Trichopterygia Illustrata et Descripta. London, 188 pp., 30 pls.

1884. Synopsis of North American Trichopterygidae. Trans. Am. Ent. Soc., **11**, pp. 113–156.

1888. Biologia Centrali-Americana. Insecta. Coleoptera. Fam. Trichopterygidae. **2** (1), pp. 126–156, pl. III.

MAYR, E.

1963. Animal Species and Evolution. Harvard Univ. Press. xiv+797 pp.

NIETNER, J.

1857. Descriptions of New Ceylon Coleoptera. Ann. Mag. Nat. Hist. (2), **19**, pp. 376–388.

PAULIAN, R.

1952. IV. Coleopteres. *In* Delamare-Deboutteville, C. and R. Paulian, Recherches sur la faune des nids et des terriers en Basse Côte d'Ivoire. Encycl. biogéogr. écol., Paris, **8**, pp. 90–103.

Reichle, D.
Some Pselaphid Beetles with Boreal Affinities and their Distribution Along the Postglacial Fringe. (In press.)

Rensch, B.
1948. Histological Changes Correlated with Evolutionary Changes in Body Size. Evolution, **2**, pp. 218–230.

Riegel, G. T.
1963. The Distribution of Zorotypus hubbardi (Zoraptera). Ann. Ent. Soc. Am., **56**, pp. 744–747.

Riegel, G. T. and M. B. Ferguson
1960. New State Records of Zoraptera. Ent. News, **71**, pp. 213–216.

Suomalainen, E.
1962. Significance of Parthenogenesis in the Evolution of Insects. Ann. Review Ent., **7**, pp. 349–366.

Vaurie, Patricia
1952. Insect Collecting in the Bimini Island Group, Bahama Islands. Am. Mus. Novit., No. 1565, pp. 1–24.

White, M. J. D.
1954. Animal Cytology and Evolution (2nd ed.). Cambridge Univ. Press, xiv+454 pp.

Wollaston, T. V.
1867. Coleoptera Hesperidum. London, xxxix+285 pp.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 JANUARY 30, 1967 No. 3

The Flower-Adapted Tongue of a Timaliinae Bird and Its Implications

AUSTIN L. RAND

CHIEF CURATOR, DEPARTMENT OF ZOOLOGY

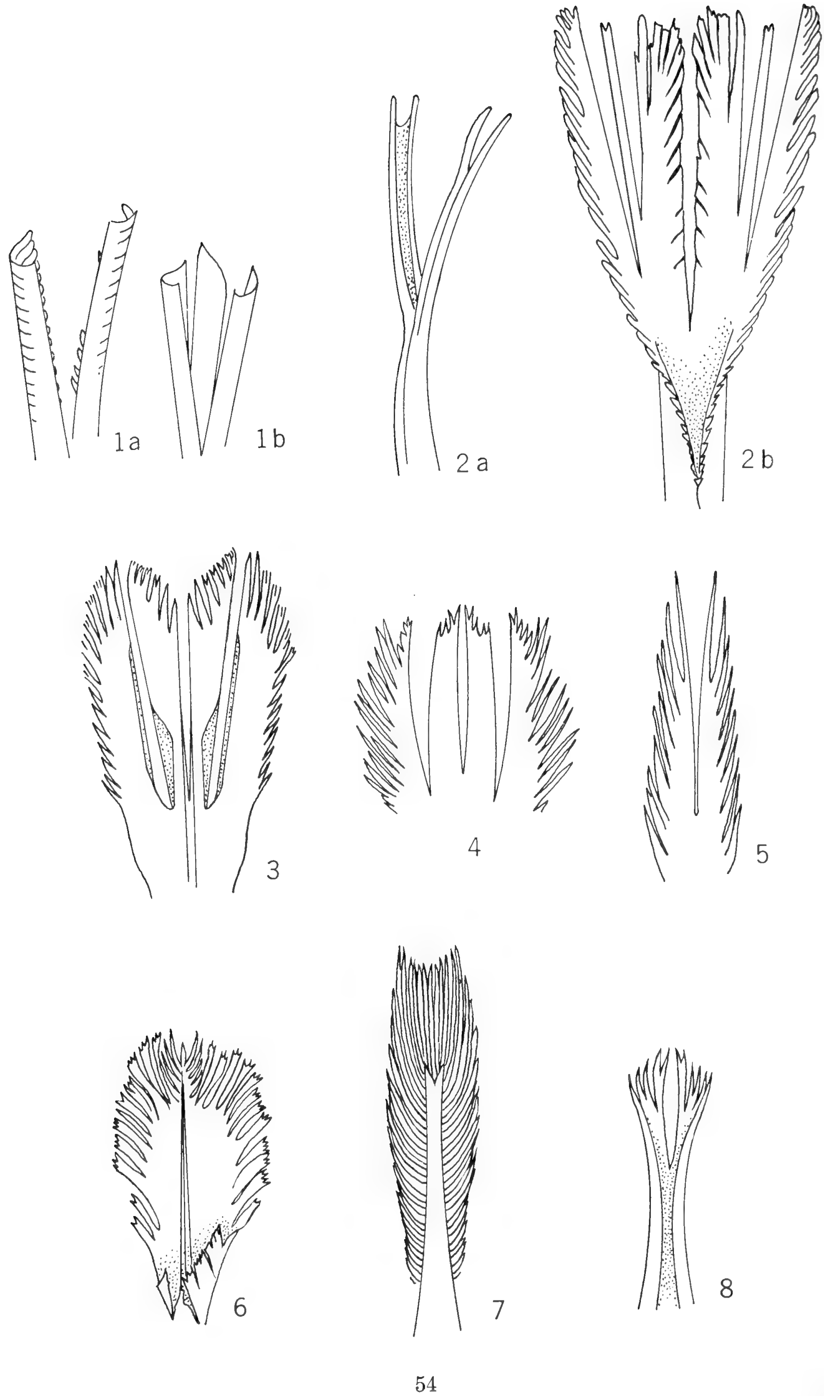
Myzornis is a monotypic genus for a small, little known, passerine bird of higher altitudes in the Himalayas. The genus is traditionally placed in the Timaliidae and has been associated with *Chloropsis* and *Aegithina* by Stuart Baker (1922, p. 345), perhaps because of its predominately green coloration, and with *Leiothrix* and *Cutia* by Delacour (1946, p. 29), presumably because of the red, black and white pattern in the wing. In the latest treatment of the family (as a subfamily) by Deignan (1964, X, p. 428), *Myzornis* is placed in a group, "Genera sedis incertae," along with a small miscellany of other nonconformists, at the end of the Timaliinae. In the rather slender, but only slightly elongated bill, *Myzornis* is only somewhat different from certain other Timaliinae genera such as *Yuhina*.

In addition to the above, the most outstanding features of *Myzornis* seem to be the black and green, scale-like pattern of the head and the nectar-adapted tongue. Though the brush-tipped character of the tongue was mentioned as early as 1890 (Murray, p. 173), there seems to be no detailed description of the tongue, and it seemed worthy of examination for possible clues to relationships. Thanks to the efforts of Dr. Robert L. Fleming, Superintendent of the United Christian Medical Mission to Nepal and an Associate of the Field Museum of Natural History, the Museum has a series of these birds with their dried tongues, and Dr. Fleming's notes on the species, habits.

The tongue of *Myzornis* proves to be not only brush-tipped, but curled-tubular, frayed and split (fig. 2). The tongue is horny and as long as the bill. In the dried tongue the basal portion is flat and anteriorly the edges soon curl in to form a tube. In the middle third

Library of Congress Catalog Card Number: 66–29539

No. 1017


1a
1b
2a
2b
3
4
5
6
7
8

of the tongue this curling seems to continue until two parallel tubes are formed. In the terminal third the tongue is split along the midline and has the tips frayed and curled to give two more or less tubular branches with brush tips.

When the tongue is softened in water and flattened, the structure of the tip appears as follows (fig. 2): each half of the tip has a feather-like structure with a rachis-like, horny "shaft" and vane-like margins frayed on each edge but more so on the outer web. In addition, the terminal end of the rachis-like shaft is frayed or split into a dense tuft of straight bristles. These apparently remain straight and in the dried tongue are more or less enclosed by the curled bristles of the margins. This appears to be a tongue highly specialized for flower feeding—tubular for nectar, fringed for picking up small insects and nectar, and with a tuft of straight bristles at the tip for probing. This type of tongue is not reported elsewhere in the Timaliidae.

The little we know of *Myzornis*' feeding and behavior is from a series of short notes recorded over the years. *Myzornis* is said to have been found on the ground, on tree trunks climbing like a creeper, in bushes, in the lower limbs of trees, and in treetops. It is recorded as solitary, occurring in pairs, and in mixed parties of other small birds. It is said to sit quietly, to hop about actively, to make short sallies like a flycatcher, to hover in front of flowers and probe into them, and to alight on tree trunks and drink sap oozing from a hole in the bark. Stomach contents are reported as small insects and berries (see especially Jerdon, 1863, p. 263; Stevens, 1924, p. 739; and Salim Ali, 1962, p. 189).

Such a composite picture is not unusual in compiling data on birds from lesser known parts of the world, but it is discouraging when attempting to outline the normal and characteristic aspects of a species behavior. Can the bird be so versatile, especially in view of its nectar-adapted tongue? However, the recorded observations

---

FIG. 1. Diagrammatic views of distal portions of tongues, flattened, of eight songbird families, to show differences in detail of flower-feeding adaptation.

1. Nectariniidae: (a) *Nectarinia jugularis;* (b) *Aethopyga.*
2. Dicaeidae: (a) *Dicaeum trigonostigma;* (b) *D. nigrilore.*
3. Meliphagidae: (*Apalopteron*).
4. *Promerops cafer.*
5. Coerebidae: *Cyanerpes cyanea.*
6. Drepaniididae: *Vestiaria coccinea.*
7. Chloropsiedae: *Chloropsis.*
8. Zosteropidae: *Zosterops simplex.*

References for drawings: 1, Scharnke. 2a, Gadow. 2b, Rand. 3, Deignan, 1958. 4, Scharnke. 5, Lucas. 6, Scharnke. 7, specimen. 8, Beddard.

do corroborate the evidence of the tongue that *Myzornis* is a flower feeder at least part of the time. That flower-feeding is characteristic of the species is indicated by the Nepal name that translates "mountain honeysucker" (Jerdon, 1863).

Dr. Fleming writes that he found *Myzornis* common on the east Nepal border between 7,000 and 8,000 feet altitude where it was usually in the branches of large oaks, or in bamboo clumps in forest glades. When the bird was sitting quietly on a perch it reminded him of a *Chloropsis*, but when it was excited it behaved like a sunbird, hopping about, turning its head from side to side, and calling ". . . chi – chi . . ." all in the same pitch. Once the voice was learned it was easy to locate the birds by ear.

Before I had examined the tongue of *Myzornis* I had considered the possibility of this bird being an aberrant member of one of the flower-feeding groups of birds occurring in southern Asia, the specialized sunbirds (Nectariniidae), or the less specialized flowerpeckers (Dicaeidae), white-eyes (Zosteropidae), leaf birds, i.e., *Chloropsis* (Chloropseidae), or even an extralimital member of the specialized honeyeaters (Meliphagidae) of the Australian area. Until these possibilities had been explored, I was inclined to consider *Myzornis* as a bird of status "sedis incertus," as Deignan did. But the tongue, while as specialized a flower-feeding organ as that of any of the above groups, differs in detail of structure which does not suggest relationship with any of them. (Comparisons follow.)

As an indicator of relationship, the flower-feeding tongue of *Myzornis* has proved of little value. The role of the tongue in taxonomy has been discussed a number of times, for instance, by Gardner (1925) for birds in general, by Amadon (1950, pp. 221–224) for the Hawaiian honeycreepers and possible relatives, and Rand (1961) for flowerpecker-honeyeater possible relatives. Sometimes it is useful in confirming relationship indicated by other characters (Deignan, 1958); sometimes it suggests relationship, as between the Dicaeidae and Nectariniidae and Meliphagidae (Rand, 1961); and sometimes it is not useful, as in the present instance.

Otherwise the only outstanding indicator of relationship of *Myzornis* is the greenish color and the variegated pattern of the wing and tail. This seems to suggest relationships with that part of the Timaliidae represented by *Leiothrix-Minla* where Delacour (1946) placed it. The diversification of general habits shown by these birds as outlined by Salim Ali (1962) also accords with the recorded habits of *Myzornis*, though only the related, duller-colored genera *Yuhina* and *Heterophasia* are recorded as regular flower feeders.

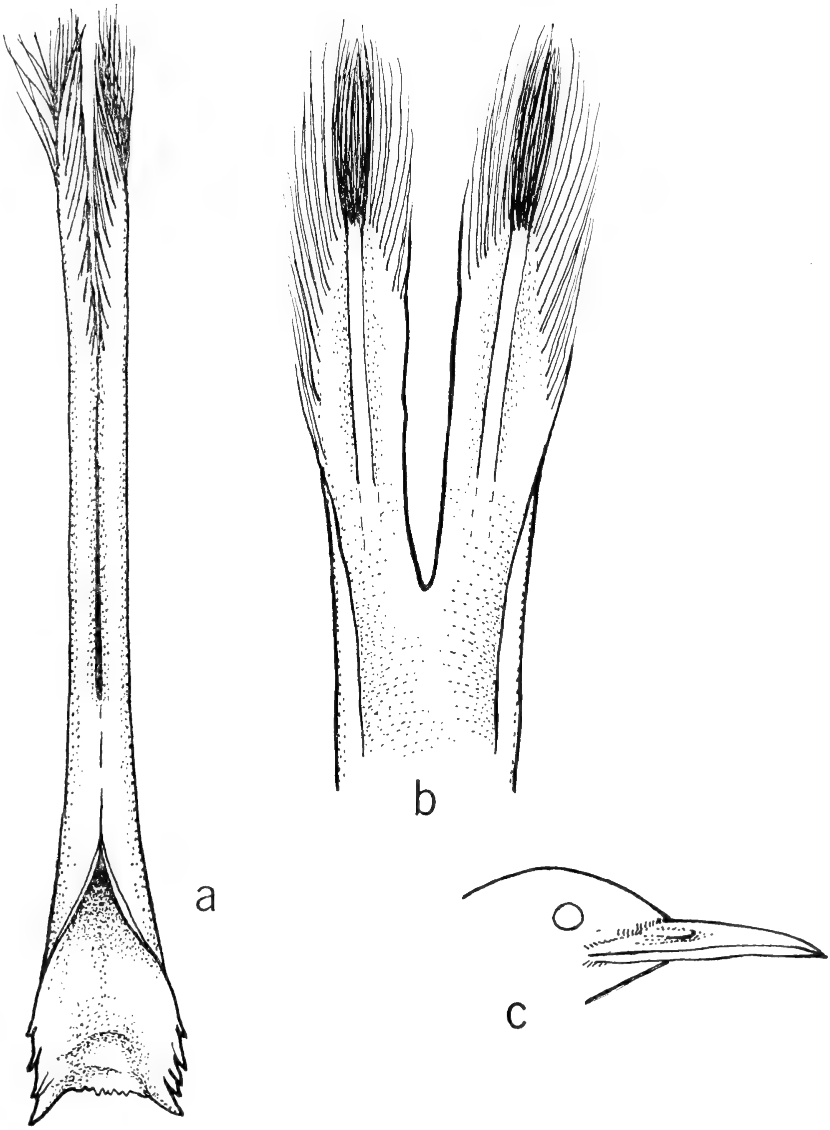


FIG. 2. *Myzornis pyrrhoura.* (a) Whole tongue seen from above; length about 16 mm.; (b) Enlargement of tip, of tongue, flattened; (c) Head of bird.

Southern Asia is not the headquarters of any specialized group of flower feeders and the most specialized group of flower feeders occurring there, the sunbirds, is the result of an invasion from Africa at an earlier period. However, southern Asia is the headquarters of the species-rich and genus-rich Timiliidae which has evolved many types from jay-like to warbler and tit-like birds of various sizes, colors and patterns and bill shapes, and some of these birds have a rather wide spectrum of feeding habits, on insects, fruits and at flowers. Presumably *Myzornis* is an offshoot of the *Leiothrix-Minla-Yuhina* branch of the family, specialized in structure for flower feeding but still retaining the family diversity of feeding habits. On present evidence I would place it, as Delacour did, among the small, brightly colored and marked members of the family, near *Leiothrix*.

A certain amount of curling, splitting and fraying occurs in members of many songbird families (see Gardner, 1925). In only eight songbird families is curling, fraying, and/or splitting carried to an extreme elaboration for flower feeding. Even in these eight families not all members of each family have such pronounced modifications. While the curling in of the edges of the central part of the tongue to form a tube is common to all, extreme modification for flower feeding, the detail of the tip, in curling, in fraying along the side, and/or splitting down from the tip to give longitudinal division, varies from group to group as outlined below.

A. In the Old World there are two large songbird families most of which are flower feeders.

1. Meliphagidae. In the honeyeaters the predominate pattern is to have the tip split into four parts, each of which is frayed along one margin. However, one species with a much simpler tongue is known, *Melipotes*, of New Guinea (Scharnke, 1933, p. 355), though it still shows a rudimentary four-parted tip. Probably this is degenerate, following a switch to a predominately berry diet.

The sugar bird, *Promerops*, of South Africa, now is usually placed in the Meliphagidae, chiefly because of the four-part tip of the tubular tongue. However, both Scharnke (1932, pp. 119 and 135) and Dorst (1952, p. 192) consider it more likely to be a case of convergence. There is one feature in the *Promerops* tongue that is rather different from any Meliphagidae I have examined or seen figured. Only the two outer parts of the tip are frayed to give the brush tip. The two centered elements are not frayed and appear as if modified for probing. A perplexing problem is that if it is not

a member of the Meliphagidae other relationships are as difficult to establish.

2. Nectariniidae. The usual sunbird tongue in the large genus, *Nectarinia,* has the tip split into two parts each of which is curled to form a tube. There is no obvious brush tip, though some slight fraying is evident under moderate magnification along the inner (not the outer) edges of each segment as Scharnke (1932, p. 117) shows it. However, Gadow (plate XVI, figs. 8–10) shows this fimbrication more accentuated. *Aethopyga* has a third flat element at the tip that helps complete the tubes (Scharnke, 1932, p. 117).

One species, however, *Anthreptes singalensis,* has the tongue flat with its edges slightly frayed, and with very little splitting at the tip, thus quite unlike the usual condition (Gardner, 1925, fig. 139).

B. In three other Old World families most species are better known as berry eaters and their most developed nectar-feeding adaptations are known in only a few species.

3. Dicaeidae. The flowerpeckers, in a few specialized species, have the tongue tip either (a) split into two parts each of which curls to form a tube, without fraying, or (b) splits into four parts each of which is frayed on one margin and curled.

Thus one condition recalls that of the sunbirds, the other approaches that of the honeyeaters. This may indicate an actual relationship. Some other flowerpeckers (*Melanocharis*), feeding on berries, have a standard, flat, passerine bird tongue.

4. Zosteropidae. In white-eyes with specialized tongues there is a median splitting at the tip, accompanied by lesser splitting and/or fraying to give a brush tip. This seems a less specialized condition than any of the above.

5. Chloropseidae. In the leaf bird, *Chloropsis,* the tip is more or less entire with a fimbriate fringe along the sides and around the tip, the whole curling to form a single tube.

6. Timaliidae. Among the babblers only one species, *Myzornis,* is known to have a flower-feeding tongue as described above. The tip is split in two with each half frayed on each side, and a central "shaft" which splits up to form a brush tip enclosed by the curling of the lateral fraying into a tube.

C. In the New World there are two songbird families with pronounced flower-adapted tongues in some species.

7. Coerebidae. The American honeycreepers have for their usual advanced pattern the tip of the tongue deeply cleft or split and

each half frayed on the outer side only. Curling apparently is pronounced.

8. Drepaniidae. The Hawaiian honeycreepers apparently have two advanced conditions: (a) the tongue is simply curled into a single tube, with little or no fraying or splitting, or (b) with little or no splitting, the edges are frayed and curl to form a single tube.

Among the songbirds, nectar adaptation has obviously arisen separately in each of the eight outstanding cases, discussed above, that have come to my attention. Other families, notably Parulidae and the Icteridae, have members with a tendency toward a nectar-adapted tongue. Such convergence is not surprising, and is also seen in bill shape in other groups: the broad flat bill for flycatching; slender bill for gleaning small insects; a hook at the tip of the bill for holding larger prey; and a heavy conical bill for seed eating.

More interesting is the fact that, beyond the simple gross adaptation of a tubular tongue for flower feeding, the finer details differ in detail of structure of the tip of the tongue for each specialized songbird family. A similar function is achieved by a similar but not identical structural change.

REFERENCES

Ali, Salim
1962. The Birds of Sikkim, pp. 1–414. Oxford University Press.

Amadon, D.
1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Amer. Mus. Nat. Hist., **95**, pp. 157–262.

Baker, E. C. Stuart
1922. Fauna Brit. India. Birds, **1**, pp. 1–479. London.

Beddard, F. E.
1891. Ornithological notes. Ibis, **1891**, pp. 510–512.

Deignan, H. G.
1958. The systematic position of the bird genus *Apalopteron*. Proc. U. S. Nat. Mus., **108**, pp. 133–136.
1964. Peters Check-list of Birds of the World, **10**, p. 428. Cambridge, Mass.

Delacour, J.
1946. Les Timaliines. L'Oiseau et R. F. O., **16**, pp. 1–36.

Dorst, J.
1952. Contribution a l'étude de la langue des Meliphagides. L'Oiseau et R. F. O., **22**, pp. 185–214.

Gadow, H. H.
1890–1900. *In* Aves Hawaiiensis, by S. B. Wilson and A. H. Evans, pp. 219–249, pl. III, fig. 56. London.

GARDNER, L. L.

1925. The adaptive modifications and the taxonomic value of the tongue in birds. Proc. U. S. Nat. Mus., **67**, art. 19, pp. 1–49.

JERDON, T. C.

1863. The Birds of India, **2**, pp. 1–439. Calcutta.

LUCAS, F. A.

1895. Notes on the anatomy and affinities of the Coerebidae. . . . Proc. U. S. Nat. Mus., **17**, pp. 299–312.

MAYR, E., and D. AMADON

1947. A review of the Dicaeidae. Amer. Mus. Nov., no. 1360, pp. 1–32.

MURRAY, J. A.

1890. The avifauna of British India, **2**, pp. 1–838. London.

RAND, A. L.

1961. The tongue and nest of certain flowerpeckers (Aves: Dicaeidae). Fieldiana: Zool., **39**, pp. 581–587.

SCHARNKE, H.

1932. Über den Bau der Zunge der Nectariniidae, Promeropidae, und Drepanididae. . . . Jour. f. Orn., **80**, pp. 114–123.

1933. Über eine ruckgebildete Honigfresser-Zunge. Jour. f. Orn., **81**, pp. 355–359.

STEVENS, H.

1924. Notes on the birds of the Sikkim Himalayas. Jour. Bombay Nat. Hist. Soc., **29** (pts. 3–4), p. 739.

FIELDIANA · ZOOLOGY

Published by
FIELD MUSEUM OF NATURAL HISTORY

Volume 51 | February 27, 1967 | No. 4

Systematic Status of Three Scincid Lizards (Genus *Sphenomorphus*) from Borneo

James P. Bacon Jr.
Department of Zoology, University of Chicago

Scincid lizards of the genus *Sphenomorphus* are not commonly collected in numbers because of their small size, secretive habits, and propensity for low population densities within the rain forest. Two years of intensive work by six to eight collectors in four ecologically and geographically diverse areas in Sarawak yielded but 58 specimens of six species. Fifty-three of these individuals are samples of species unknown a decade ago. Inger and Hosmer (1965) described two new species (*S. cyanolaemus* and *S. haasi*) from this material. As identification of the collection was completed, six skinks remained to which names could not be readily assigned. These six specimens are easily separable into three morphologically distinct groups. After careful comparison of these groups with the known forms of this genus from Southeast Asia and the East Indies, I believe that the evidence warrants the recognition of one new species. The remaining two groups are apparently conspecific with two previously known species. One, described in 1900 by Boulenger, is reported from Borneo for the first time. The second is apparently conspecific with a species described by Lidth in 1905 from Indonesian Borneo and heretofore known only from the holotype.

The genus *Sphenomorphus* is large and vaguely delimited. Whether or not it represents a natural group in any sense of the word is not known and will not be pursued in this brief report. These samples exhibit characters which place them in the partially synonymous taxa of the following authors: Boulenger (1887), subgenus *Hinulia* of *Lygosoma;* de Rooij (1915), section *Hinulia* of *Lygosoma;* Taylor (1922),

Library of Congress Catalog Card Number: 66–30675

genus *Sphenomorphus;* Smith (1937), section *Sphenomorphus* of *Lygosoma.* The following character states constitute the evidence for this generic assignment: supranasals absent, no fusion of dorsal head scales, frontal not broader than supraocular region, no auricular lobules, eyelids present and lower lid scaly, length of hind limb greater than distance from arm to center of eye and less than distance from arm to tip of snout.

The following abbreviations have been used: BM(NH)—British Museum (Natural History); FMNH—Field Museum of Natural History. Dr. A. G. C. Grandison kindly examined British Museum specimens and forwarded critical data to the author.

Acknowledgments.—My thanks go to Dr. R. F. Inger and Mr. Hymen Marx for their criticism and suggestions; my wife Betty and Mrs. Marion Anderson for typing of the manuscript. Mr. H. K. Voris and Miss Wilma Wallace kindly took the time to test the key.

This study was supported by the National Science Foundation (grant nos. G-6257, G-20867, and GB-1049).

Sphenomorphus maculicollus new species. Figure 1.

Holotype.—Field Museum of Natural History no. 161484. An adult male collected by Mr. William Hosmer near Sungei Pesu, Bintulu District, Fourth Division, Sarawak, Malaysia on May 22, 1964 (fig. 4).

Diagnosis.—Two anterior loreals; 8 supraoculars; a distinct dark spot on each side of the neck; no auricular lobules; 36 scale rows.

Description of holotype.—Habitus slender; snout short; head deep; limbs and digits well developed.

Head scales smooth but not polished, iridescent; rostral broad, nearly trapezoidal, forming long slightly curvilinear suture with frontonasal; latter twice as broad as long, not touching frontal, meets anterior upper loreal laterally; prefrontals well developed, separated by an azygous scale middorsally; frontal long, broadest between first supraoculars and with posterior apex between fourth supraoculars, equal to frontoparietals and interparietal in length; 8 supraoculars (counting inclusively to that scale which touches both parietal and frontoparietal), 2–3 small scales follow eighth; frontoparietals not fused, longer than interparietal; interparietal nearly as broad as long; parietals meet behind interparietal, greatest length less than twice greatest width; no nuchals.

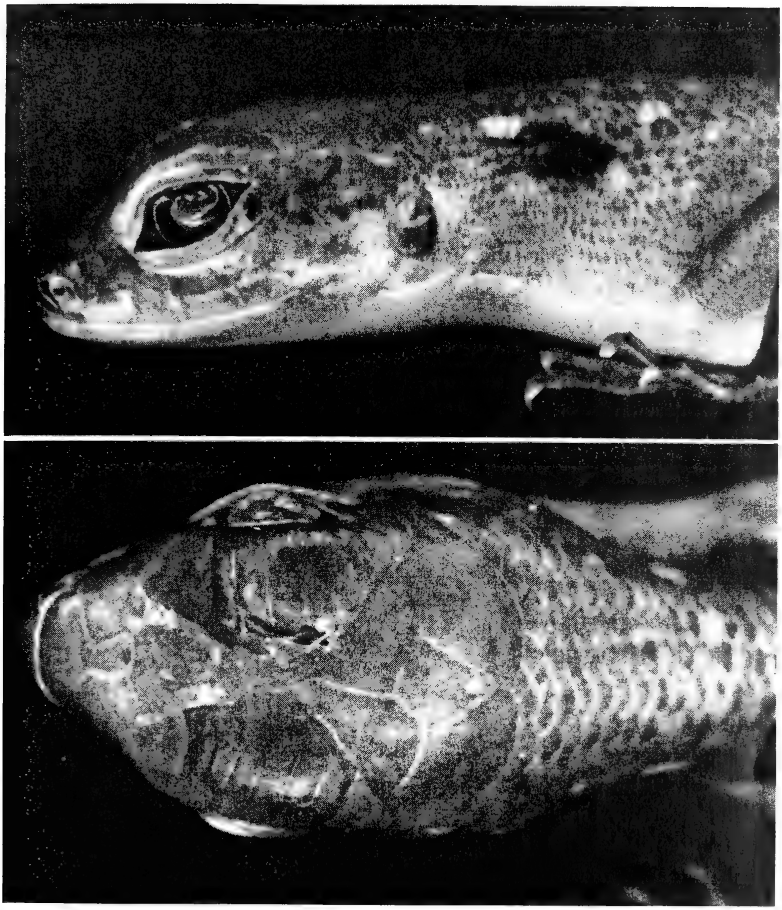


FIG. 1. Holotype of *Sphenomorphus maculicollus* (FMNH 161484).

Nostril in single nasal; no supranasal; 2 anterior loreals; 2 posterior loreals; one preocular; 5 supralabials (to posterior corner of eye), first smallest, fourth below lens of eye; circumorbital ring of small scales separates the supralabials from lower eyelid; 15/16 supraciliaries; one slightly enlarged temporal borders parietal laterally; tympanum slightly ovoid, erect, slightly sunken, height equals half length of eye opening and three-fourths distance from nostril to anterior corner of eye.

Posterior border of mental straight, closer to posterior than to anterior edge of first supralabial along margin of mouth; 6 infralabials

(to infralabial touching last supralabial), first longest, sixth shortest; azygous postmental two-thirds as long as broad; 3 pairs of chin shields, first pair longest, juxtaposed, second pair separated by one scale, third pair separated by 3 scales.

Scales of body in 36 rows at point midway between vent and axilla, shiny, iridescent, with very fine striae or pitting; lateral scales slightly smaller than dorsals and ventrals; 90 scales between mental and vent; 2 enlarged preanal plates, width equal to that of anterior chin shield.

Scales of ventral surfaces of limbs slightly smaller than those of dorsal surfaces; palms and soles covered with smooth, flat, polygonal to ovoid, juxtaposed scales; 17/18 broad, smooth lamellae beneath fourth toe, 13 beneath fourth finger.

Proximal 10 rows of subcaudals small; posterior to this point, subcaudals larger than neighboring scales.

Description of coloration taken from field notes and laboratory observations; specimen only slightly faded in alcohol. Head light brown dorsally, all scales sprinkled with minute dark brown spots, laterally brown grades to white on supralabials, some aggregations of dark spots along labial margins. Chin and throat immaculate white.

Scales of dorsal and dorsolateral surfaces light brown; varying density of pigment spots gives appearance of irregular pattern; dorsolaterally there is a row of small white spots; below and between first two spots on side of the neck is a single dark spot roughly 13 scales in area; laterally there are some scattered white spots; ventrolaterally the tan ground color gives way to the lighter ventral coloration; dorsal surfaces of limbs are light brown with small irregular white spots; white spotting on tail forms closely spaced vertical bars, flecked with dark brown, posteriorly the bars meet middorsally, interspaces are lighter brown. All ventral surfaces are immaculate white except posterior two-thirds of tail with dark brown mottling, and gray palms and soles.

Measurements (mm.).—Snout-vent, 49; tail, 107; hind limbs, 20; axilla-snout, 20; head length (to ear opening), 9.7; head depth (behind eye), 6.2.

Comparisons.—For comparative tables of data on Bornean *Sphenomorphus* see Inger and Hosmer (1965). This is the first specimen of *Sphenomorphus* from Borneo to possess eight supraoculars; 50 per cent of specimens of *S. multisquamatus* and occasional specimens of *cyanolaemus* and *sabanus* have seven. Number of scale rows clearly

distinguishes *multisquamatus* (42–49) and *haasi* (41–42) from *maculicollus* (36). The species *sabanus* and *cyanolaemus* sometimes have as few as 37–38 scale rows; *sabanus* has strongly barred labials and no dark markings of any kind on the neck, while the males of *cyanolaemus* have a dark blue throat and no white spots dorsally. The Bornean species *S. shelfordi* (Boulenger), *S. buttikoferi* (Lidth), *S. hallieri* (Lidth), *S. alfredi* (Boulenger), and *S. tenuiculum* (Mocquard) all possess but four supraoculars. The Papuan forms *S. stickeli stickeli* Loveridge, *S. s. melanopleurus* Inger, and *S. jobiensis* Meyer have 21 fourth toe lamellae as does *S. variegatus* (Peters) from Mindanao. A few specimens of *stickeli* have eight supraoculars.

Sphenomorphus stellatus (Boulenger)

Lygosoma stellatum Boulenger, 1900, Ann. Mag. Nat. Hist., **6**, p. 192—type locality: Perak: Larut Hills; 1912, Fauna Malay Pen., p. 87; Smith, 1921, Proc. Zool. Soc. London, **1921**, p. 431; 1935, Fauna Brit. India, Rept. Amph., **2**, p. 284.

Sphenomorphus stellatus, Mittleman, 1952, Smithsonian Misc. Coll., **117**, p. 30; Taylor, 1963, Univ. Kansas Sci. Bull., **44**, p. 1008.

Lygosoma annamiticum Boettger, 1901, Ber. Senckenberg. Ges., **1901**, p. 47—type locality: Annam: Phuc-Son.

Taxonomic notes.—This form was described from specimens collected in the Larut Hills of Perak, Malaya (Boulenger, 1900). It has 24 scale rows, the two dorsalmost rows twice as broad as long, oval ear opening slightly smaller than eye with no auricular lobules, and "Bronze-colour above, spotted all over with black and white . . . lower parts bluish or greenish white." According to the measurements given by Boulenger (1900) the ratio of the fore and hind limbs to body length are high (see Table 1).

On December 14, 1962, Mr. F. W. King collected a specimen of *Sphenomorphus* in Sarawak which is similar to *S. stellatus* (Boulenger). The specimen from Sarawak possesses 24 rows of smooth scales with the dorsalmost rows enlarged. The example from Sarawak differs from the syntypes in possessing the following character states: nearly immaculate bronze dorsum, strongly patterned chin and throat, fewer subdigital lamellae on fourth toe and fourth finger, and shorter limbs (see Table 1). The magnitude and number of these morphological differences along with the geographical isolation of these populations suggests genetic differentiation to the extent that population interbreeding would not be possible. This would warrant specific recognition of the Sarawak specimen.

TABLE 1.—Ratios, scale counts, and relationships of five populations of *Sphenomorphus stellatus* (Boulenger).

	South Viet Nam (Dalat and Phuc-Son)	Thailand	Borneo	Malaya
Fourth toe lamellae	20–22	18	19	20–23
Fore limb/snout-vent	0.21–0.26	0.28	0.24	0.33
Hind limb/snout-vent	0.36–0.38	0.35	0.36	0.45
Ear opening $>$ or $<$ $\frac{1}{2}$ eye opening	$<$	$>$	$<$	$<$
Frontal touching fronto-nasal	+	–	–	–
Dorsal pattern rows of spots	+	+	–	+
Venter immaculate	–	+	–	+
Pairs nuchals	3–4	2–3	3	2–3
Scale rows	24	22	24	24
Upper temporal	large	large	large	large
Middorsals	broad	broad	broad	broad

Smith (1935) synonymized *L. annamiticum* Boettger with *L. stellatum*. Boettger's sample (2 individuals) has 24 scale rows, dorsalmost two rows enlarged, and the distinctive dorsal color pattern. These specimens, from Phuc-Son, N. Annam are characterized by the separation of the prefrontals and the presence of markings on the throat.

Taylor (1963) collected a specimen in the isolated highland region of southeastern Thailand at Khao Sa Bap (=Khao Sebap or Khao Sabap), Chanthaburi Province. He noted some differences between his specimen and Smith's (1935) description of *L. stellatum* Boulenger, but considered the specimen conspecific with those of Boulenger and Smith.

Grandison (*personal communication*) has provided the following data on the syntypes and a specimen from Annam. Both syntypes, BM(NH) 1946.8.3.26 and 1946.8.17.10, have enlarged temporals (see fig. 2) and the height of the tympanum is less than one-half the length of the eye opening. The tympanum is described as "broadly oval." The example from Dalat, Annam, BM(NH) 1921.4.1.158, also has enlarged temporals and there is some "dark banding at the edges of the labials and gulars." The tympanum is "round" and equal in height to one-half the length of the eye opening.

Grandison also notes that the enlarged vertebral series is anteriorly more distinct from the adjoining rows in the Annam specimen when compared with the syntypes. That the characters form a mosaic distribution among these five small samples is shown by Table 1.

There is no way at present to determine whether these five populations represent five species, a single polytypic species, or some intermediate combination of genetic relationships. The presence of the following suite of characters in all five geographic areas suggests that this may be a single species: enlarged temporals, low number of scale rows, enlarged middorsal scale rows, four supraoculars, and nuchals present. The hypothesis that these populations represent a polytypic species seems biologically reasonable and taxonomically conservative. The apparent mosaic of some characters may be the result of evolution in response to differing selective pressures upon relatively small populations in isolated or partially isolated upland communities. The Bornean population is not recognized as differing taxonomically from the mainland populations. The mosaic nature of the character state distributions and small sample sizes are persuasive arguments in favor of this treatment.

Diagnosis.—Scales in 22–24 rows midway between axilla and groin; upper posterior temporals greatly enlarged; 4 supraoculars; enlarged middorsal scale rows; throat with or without barred pattern; dorsum light brown, with or without rows of spots; limbs moderate.

Description of Bornean example.—Habitus slender, body long, limbs moderately strong, head with moderately steep loreal region, snout pointed, head distinguishable from neck, tail (broken) round.

All scales smooth and polished, somewhat iridescent, except on palms and soles; rostral large, curves onto dorsal and lateral surfaces of snout, suture with frontonasal short, one-third width of frontonasal; width of latter less than twice length, touches anterior loreal laterally; prefrontals large, juxtaposed, suture more than one-half length of scale; frontal longer than parietals and interparietal, blunt posterior apex between second supraoculars; 4 supraoculars, first longest, second widest; frontoparietals not fused, contact supraoculars 2–4 laterally; interparietal shorter than frontoparietals, only slightly longer than broad; parietals meet behind interparietal along short suture, greatest length more than twice greatest width.

Nostril low in nasal; no supranasal; 2 loreals, anterior taller than long, posterior roughly as tall as long; 3 presuboculars, first large, beneath lower preocular; upper and lower preocular present, latter largest; 8 supraciliaries, first and eighth largest; 2 anterior and 3 posterior suboculars; 5/6 supralabials, fourth or fifth beneath lens of eye; 2 small lower temporals; one small anterior and one very large posterior upper temporal; tympanum round, diameter less than half length of eye opening.

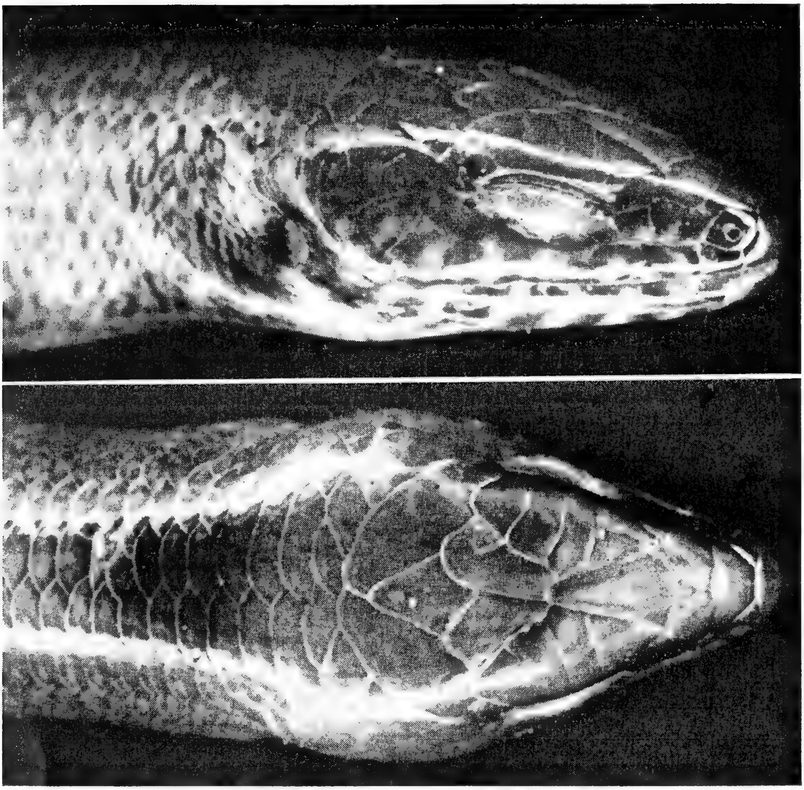


FIG. 2. *Sphenomorphus stellatus* (FMNH 138544).

Mental width roughly twice length, posterior border straight, at margin of mouth meets first supralabial at midpoint; 6 infralabials, first shortest, fifth longest; single postmental, length more than twice width; 3 pairs of chin shields (enlarged scales bordering infralabials), first pair juxtaposed, second separated by one scale, third separated by 3 scales; one pair of elongate postgenials follows last pair of chin shields, separated by 6 scales.

Six nuchals in 2 transverse rows; 2 middorsal scale rows more than twice as broad as long, laterals and ventrals roughly equal, length more than one-half width, scales in 24 rows midway between axilla and groin; scales of anterior surfaces of limbs larger than those of posterior surface; palms and soles with elongate, juxtaposed, obtusely keeled scales; subdigital lamellae obtusely keeled, 19 beneath fourth toe, 12 beneath fourth finger, a bluntly bicarinate scale precedes the subdigital lamellae of digits 3 and 4 of the hand (see Boettger, 1901).

Two enlarged preanal plates; subcaudals broader than neighbors.

Color in preservative: all scales of dorsal surfaces bronze, covered with pinpoints of dark pigment, no spots or pattern.

Labials dark, all except first with a white spot; mental, postmental, and chin shields white with dark bands on posterior one-third which overlaps onto anterior tip of following scale; throat with 7–8 distinct longitudinal, dark bands between scale rows, bands fade in pectoral region; abdomen whitish with some pinpoints of dark pigment on each scale; preanals darkened by concentration of pigment; some light flecks appear on side of neck and thorax, tan coloration gives way to whitish ventrolaterally.

Limbs bronze with white flecks dorsally, whitish ventrally; palms and soles gray; tail stump bronze with fairly distinct vertical rows of 3–4 white spots laterally, whitish ventrally with irregular dark line of pigment spots between subcaudals and neighboring scales.

Comparison.—Five other species of Bornean *Sphenomorphus* have four supraoculars. They are *S. tenuiculus* (Mocquard), *S. shelfordi* (Boulenger), *S. buttikoferi* (Lidth), *S. hallieri* (Lidth), and *S. alfredi* (Boulenger). None of these species has enlarged middorsal rows. *Sphenomorphus shelfordi* has 32 scale rows and 28 fourth toe lamellae; *tenuiculus* has 26 scale rows, 24 fourth toe lamellae and no nuchals; *buttikoferi* has 21–23 fourth toe and 15–16 fourth finger lamellae. *Sphenomorphus hallieri* has very small parietals which do not contact the supraoculars and two pairs of chin shields; *alfredi* has 7–12 fourth toe lamellae and 28–30 scale rows. Inger has recently re-examined the types of all five species and the counts given here are his.

Four species from New Guinea have four supraoculars and nuchals. *Sphenomorphus minutus* (Meyer) has 22 scale rows, 15 fourth toe lamellae, prefrontals very small and widely separated, and a dorsal pattern of spots and streaks; *Sphenomorphus nototaenius* (Boulenger) has 24 scale rows with two enlarged vertebral rows and 18 fourth toe lamellae; however, the prefrontals do not meet, there is no greatly enlarged temporal, and there is a dorsal pattern of streaks and an immaculate venter. *Sphenomorphus elegantulus* (Peters and Doria) and *S. nigrolineatus* (Boulenger) have 26–28 rows and both have divided subdigital lamellae.

Localities.—FMNH no. 138554; an adult male collected by Mr. F. W. King near Nanga Tekalit on the Mengiong River, Kapit District, Third Division, Sarawak, Malaysia on December 14, 1962; see Figure 4.

Sphenomorphus hallieri (Lidth)

Lygosoma hallieri Lidth, 1905, Notes Leyden Mus., **25**, p. 197—type locality: Borneo: Putus Sibau; de Rooij, 1915, Rept. Indo-Austr. Arch., **1**, p. 210.

Taxonomic notes.—The third sample, consisting of four specimens, was similar enough to the original description of *Sphenomorphus hallieri* (Lidth) to warrant further investigation. Dr. Hoogmoed kindly allowed me to examine the holotype, Leiden 4456, the only known specimen. The species is distinguished from all other known Bornean skinks by the separation of the parietals from the supraoculars. I

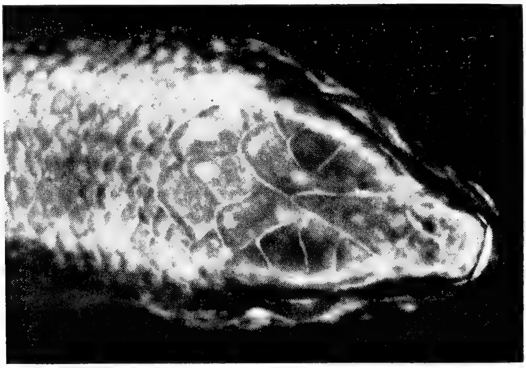


FIG. 3. *Sphenomorphus hallieri* (FMNH 161486).

believe the sample from Sarawak to be conspecific with the holotype of *hallieri* (see Table 2 and following redescription). Measurements and ratios of holotype are in parentheses. Also see Figure 3.

Diagnosis.—Prefrontals juxtaposed; parietals small, separated from supraoculars; tympanum slightly sunken, without auricular lobules; 4 supraoculars; 36–39 scale rows; limbs moderately developed, hind limbs longer than distance between anterior corner of eye and the forelimb; 2 pairs of chin shields.

Description.—Habitus slender; tail round (slightly compressed in type), head scarcely distinct from neck; snout blunt; limbs and digits not greatly reduced.

All scales except those of palms, soles and lamellae smooth and polished; rostral hexagonal, breadth equals 3 times height, suture with frontonasal straight, roughly equal to two-thirds width of frontonasal; latter nearly trapezoidal, length equals one-half width, meets anterior loreal and nasal laterally; prefrontals juxtaposed, suture

TABLE 2.—Measurements (mm.) of known specimens of *Sphenomorphus hallieri* (Lidth).

	Leiden 4456	FMNH 161486	FMNH 161485	FMNH 161488	FMNH 161487
Snout-vent	41	41	40	44	21
Axilla-groin	21	21	21	23	10
Axilla-snout	16	15	16	16	9
Head (to posterior edge of tympanum)	7.9	7.6	7.3	8.1	5.2
Fore limb	10	9	9	10	5½
Hind limb	14	13	15	15	7½
Fore limb to anterior corner of eye	12.5	12.9	12.9	13.4	7.2
Sex	?	♀	♀	♂	juv.

length more than half scale length, meet anterior and posterior loreals laterally; frontal width 0.60–0.67 (0.60) times its length, posterior apex blunt, length roughly equals length of frontoparietal and interparietal together, but greater than interparietal and parietal together; 4 supraoculars (to suture between frontoparietal and scale separating parietals from the supraoculars); 2 frontoparietals; interparietal 4-sided, width roughly 0.8 length; parietals small, meet behind interparietal, diagonal length equals 1.5–2.1 times greatest width, diagonal length less than diagonal length of frontoparietals; a slightly enlarged scale separates the parietal from the fourth supraocular; one specimen (FMNH 161485) has one nuchal, the others have none.

Nostril in single nasal; no supranasal; two loreals, both taller than long, posterior slightly longer than anterior; 5–6 (5) supralabials, fourth or fourth and fifth below lens of eye; 9–10 (9/10) supraciliaries; 3–4 small preoculars; 2 slightly enlarged presuboculars precede a complete subocular ring of small scales which separates the supralabials from the lower eyelid; no enlarged temporals; tympanum definitely but not deeply sunken, height is slightly more than half the length of the eye opening and more than three-fourths the distance between the nostril and the anterior corner of the eye.

Posterior border of mental nearly straight, meets first supralabial near its anterior edge; 5 infralabials, second longest, fifth shortest; azygous postmental, length 0.57–0.71 width; 2 pairs of enlarged chin shields, first juxtaposed anteriorly, second and posterior portion of first separated by a single scale; elongate postgenials follow 6 of 7 undamaged chin shields series, contact infralabials, roughly one-third width of and equal to length of second chin shield.

Scales of the body are in 36–39 (36) rows, smooth, polished (iridescent in Sarawak specimens); ventrals 66–76 (76) mental to preanal inclusively, slightly larger than dorsals; 68–70 (70) dorsal scales

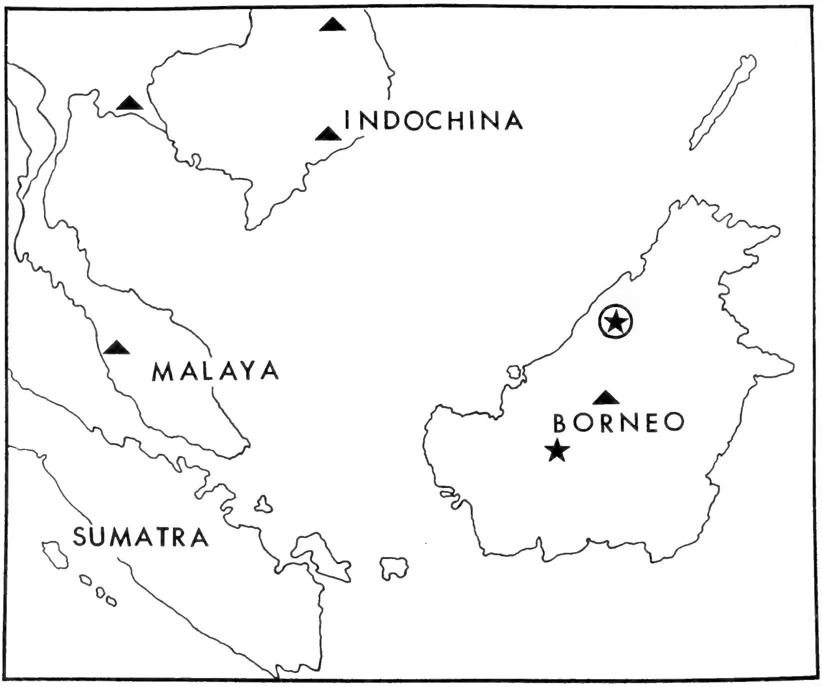


FIG. 4. Triangles show localities of *Sphenomorphus stellatus;* stars show localities of *Sphenomorphus hallieri;* circle shows type locality of *Sphenomorphus maculicollus.*

between parietal and the level of the posterior surfaces of the thigh; 2 scales which precede the vent are slightly larger than adjoining scales.

Scales of the anterior surface of the hind limb larger than those of posterior surface; palms and soles covered with polygonal, juxtaposed scales, each with a blunt, low, distally directed elevation; 12–14 (14) broad, smooth lamellae beneath fourth toe, distal ends slightly elevated; 8 lamellae beneath fourth finger; claws neither strong nor long.

Proximal two-thirds of tail without any enlarged subcaudals, distal one-third with enlarged subcaudals.

Coloration in life of FMNH 161485: medium dark brown above, anterior part of body reddish-brown; flanks white, some scales brown, side of head posterior to eye intensely pink, fading toward forelimb; white spot on each supralabial; lower parts white, throat pinkish; infralabials margined with dark brown.

The pink has faded in all preserved specimens; each dorsal scale is light brown with irregular concentrations of dark pigmented spots, on the neck these concentrations give the appearance of fine irregular lines in FMNH 161485; the other Sarawak specimens are more uniform, each dorsal scale is outlined by dark pigment; holotype much faded but retains a dark band behind the eye, interrupted by white spots and gradually fading on thorax.

Ecological note.—FMNH nos. 161486–8 were captured in hill forest under rocks and logs between 8:00 A.M. and 4:30 P.M. FMNH no. 161485 was found moving about quickly in the leaves along the bank of a stream (S. Pesu) at 8:00 P.M.

Localities.—FMNH nos. 161485–8 were collected by Mr. William Hosmer near Sungei Pesu, Bintulu District, Fourth Division, Sarawak, Malaysia. The holotype is from Putus Sibau, Indonesian Borneo (fig. 4).

Sphenomorphus multisquamatus Inger

The measurements cited by Inger (1958) as those of the holotype of *S. multisquamatus* Inger BM(NH) 1929.12.22.99 are in error. The following corrections should be noted: 5 infralabials; 101 scales between mental and vent; 20 subdigital fourth toe lamellae; snout-vent 63.5 mm.

KEY TO THE *SPHENOMORPHUS* OF BORNEO.

1a.	Four supraoculars	2
b.	Five or more supraoculars	7
2a.	Parietals in contact with supraoculars	3
b.	Parietals not in contact with supraoculars	*S. hallieri**
3a.	Scale rows 28 or more	4
b.	Scale rows 27 or less	5
4a.	Fourth toe lamellae 7–12; 28–30 scale rows	*S. alfredi***
b.	Fourth toe lamellae 28; 32 scale rows	*S. shelfordi***
5a.	Width of posterior upper temporal less than interparietal length, no nuchals	6
b.	Width of posterior upper temporal greater than interparietal length, 4–6 nuchals	*S. stellatus***
6a.	Twenty-six scale rows, 24 fourth toe lamellae	*S. tenuiculus***
b.	Twenty-four scale rows, 21–23 fourth toe lamellae	*S. buttikoferi***
7a.	Eight supraoculars, 36 scale rows	*S. maculicollus**
b.	Five to seven supraoculars, scale rows 30–49	8
8a.	Scale rows less than 36	9
b.	Scale rows 36 or more	10

* Holotype examined by Bacon.
** Holotype examined by Inger and his notes studied by Bacon.

9a. Supraoculars usually 5 (rarely 6), scale rows 32–35 . . . *S. kinabaluensis***
b. Supraoculars 6, scale rows 30–32 . . . . *S. murudensis***
10a. Dorsum dark with scattered, small, whitish (in preservative) flecks . . . . *S. haasi**
b. Dorsum not as in 10a 11
11a. Dark dorsolateral band beginning behind eye . . . . . *S. cyanolaemus**
b. No dark dorsolateral band 12
12a. Dark bars on labials absent, or when present narrower than light bars, scale rows 42–49 . . . . *S. multisquamatus**
b. Labials strongly barred, dark bars always wider than light, scale rows 38–42 . . . . *S. sabanus**

* Holotype examined by Bacon.
** Holotype examined by Inger and his notes studied by Bacon.

REFERENCES

BOETTGER, OSKAR

1901. Aufzählung einer Liste von Reptilien und Batrachiern aus Annam. Ber. Senckenberg. Ges., **1901**, pp. 45–53.

BOULENGER, G. A.

1887. Catalogue of the Lizards in the British Museum (Natural History),. Brit. Mus. Nat. Hist., **3**, xii+575 pp.

1900. Descriptions of new batrachians and reptiles from Larut Hills, Perak. Ann. Mag. Nat. Hist., **6**, pp. 186–193.

INGER, R. F.

1958. Three new skinks related to *Sphenomorphus variegatus* (Peters). Fieldiana Zool., **39** (24), pp. 257-268.

INGER, R. F., and W. HOSMER

1965. New species of scincid lizards of the genus *Sphenomorphus* from Sarawak. Israel Jour. Zool., **14**, pp. 134–140.

ROOIJ, N., DE

1915. The reptiles of the Indo-Australian Archipelago I. Lacertilia, Chelonia, Emydosauria. xiv+384 pp., Leiden.

SMITH, M. A.

1935. The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. **2**—Sauria. xiii+440 pp., London.

1937. A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. Rec. Ind. Mus., **39** (part 3), pp. 213–234.

TAYLOR, E. H.

1922. The lizards of the Philippine Islands. Philippine Bur. Sci., Manila, (17), 269 pp.

1963. The lizards of Thailand. Univ. Kansas Sci. Bull., **45**, pp. 687–1076.

FIELDIANA · ZOOLOGY

Published by
FIELD MUSEUM OF NATURAL HISTORY

Volume 51 | July 24, 1967 | No. 5

A New Colubrid Snake of the Genus *Stegonotus* from Borneo

Robert F. Inger
Curator, Division of Amphibians and Reptiles

Two specimens of *Stegonotus* are now known from Borneo, one from Mount Kina Balu (6°03′N, 116°32′E), Sabah, and one from Nanga Tekalit (1°38′N, 113°35′E), Sarawak. The skull of the latter specimen agrees with the description (Duméril and Bibron, 1854, p. 681) of the skull of *S. muelleri*, the type species. The parietal is very broad and flat with a weak median crest immediately before the supraoccipitals. The maxilla is only slightly curved and lacks a diastema; the maxillary teeth increase in size to the middle of the row, then decrease, and finally after a very short interval increase sharply at the end of the row. The palato-pterygoidal tooth row contains 49 teeth (17+32); Duméril and Bibron counted 47 (19+28). The head is slightly wider than the neck. The eyes are small and have vertically elliptic pupils. The dorsal scales are smooth and the ventrals angulate laterally. The only character in which they differ from the diagnosis of *Stegonotus* presented by Boulenger (1893) is in the absence of apical pits on the dorsal scales. In this regard, however, they resemble the type species *S. muelleri*.

The Kina Balu snake has been considered to be conspecific with the Philippine species, *S. muelleri* (Leviton, 1963). The Bornean snakes are, indeed, very similar to the Philippine form (six examined), but differ in a number of ways. As the Bornean specimens were collected in different years (1951, 1963) and from localities 560 km. apart, differences between them, on the one hand, and the Philippine snakes, on the other, are not the result of peculiarities of one brood or one extremely local population.

The ventral coloration of the Bornean snakes is homogeneous throughout the length of the body. The anterior half or three-

Library of Congress Catalog Card Number: 67-28267

No. 1028

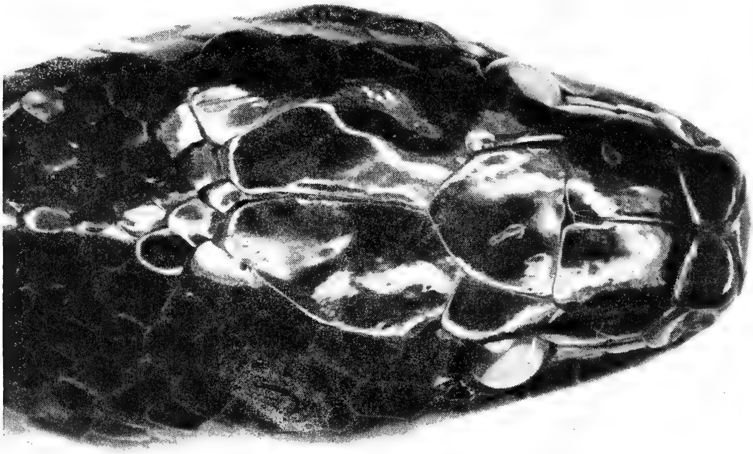


FIG. 1. Dorsal view of head of holotype (FMNH 164746) of *Stegonotus borneensis.*

fourths of each ventral is black or purplish and the posterior portion whitish. All of the Philippine snakes have whitish, unmarked ventrals in the anterior half of the body. The posterior half of the belly is uniformly black or black with white bands three to six ventrals wide.

The shapes and relative sizes of many head scales of the Bornean snakes differ from those of Philippine snakes (Table 1). The Bornean specimens have relatively shorter internasal sutures, wider frontals, shorter lower anterior temporals, and probably more squarish loreals. Not shown in Table 1 is a difference in lengths of the second chin shield, which in Philippine snakes is at least equal to the distance separating the parietal from the mouth but is shorter than that distance in the Bornean snakes.

There are also minor differences in supralabial counts (Table 2). The ventral counts (Table 2) of the Bornean snakes approach those of the Philippine snakes but the known ranges do not overlap. Subcaudal counts of the two samples may differ, but the evidence is weak. Both Bornean snakes have four rows of gulars on each side of the midline immediately behind the chin shields. Five of the Philippine snakes have three rows on each side; the sixth specimen, from Mindanao, has three rows on one side and four on the other.

TABLE 1.—Comparison of shape and relative sizes of head scales in *Stegonotus* from Borneo (*S. borneensis*) and the Philippine Islands (*S. muelleri*). All measurements are in micrometer units (6 units=1.0 mm.).

	Borneo		Mindanao	Samar		Leyte		
	USNM 130244	FMNH 164746	FMNH 53453	USNM 122203	USNM 122204	USNM 121607	FMNH 42795	FMNH 42851
Internasal suture	8	7	18	16	15	16	11	16
Prefrontal suture	24	27	37	35	32	40	22	35
Intern./prefr.	0.33	0.26	0.49	0.46	0.47	0.40	0.50	0.46
Frontal width	36	34	45	52	42	55	30	55
Frontal length	28	30	47	51	43	55	32	56
Frontal l/w	0.78	0.88	1.04	0.98	1.03	1.00	1.06	1.02
Loreal depth	7	7	10	14	11	14	8	15
Loreal length	11	8	21	22	18	22	13	22
Loreal d/l	0.64	0.88	0.48	0.64	0.61	0.64	0.62	0.68
Length of anterior temporals								
upper	30	26	37	44	40	32	21	33
lower	15	17	43	42	37	30	24	45
lower/upper	0.50	0.65	1.16	0.95	0.92	0.94	1.14	1.31

TABLE 2.—Comparison of counts in *Stegonotus* from Borneo (*S. borneensis*) and the Philippine Islands (*S. muelleri*).

	Borneo		Mindanao	Samar		Leyte		
	USNM 130244	FMNH 164746	FMNH 53453	USNM 122203	USNM 122204	USNM 121607	FMNH 42795	FMNH 42851
Sex	♀	♀	♀	♂	♀	♂	♂	♂
Snout-vent (mm.)	910	783	1253	1320	1120	1400	720	1457
Scale rows	21–17–15	21–17–15	21–17–15	21–17–15	21–17–15	21–17–15	21–17–15	19–17–15
Ventrals	219+1	194+1	222+1	232+1	222+1	231+1	231+1	227+1
Subcaudals	61+	79	80+	84+	76+	97	99	81+
Labials, upper	9	9	8	8	8	8	—	8
Labials, lower	9	10	9	10	10	10	—	9
Oculars	2–2	2–2	2–2	2–2	2–2	2–3	2–2	2–2
Temporals	2–3	2–3	2–3	2–3	2–3	2–3	2–3	2–3
Maxillary teeth	13+2	14/15+3	14+3	—	15+2	15+2	14+2	14+2

TABLE 3.—Comparison of three forms of *Stegonotus*.

Range	*dumerili* Philippines	*muelleri* Philippines	*borneensis* Borneo
No. examined	6[1]	6	2
Upper labials	8–9	8	9
Lower labials	9	9–10	9–10
Oculars	2+2	2+2	2+2
Temporals	2+3	2+3	2+3
Scale rows			
on neck	19	21	21
mid-body	17	17	17
Ventrals			
females	195–214(4)	222(2)	194–219(2)
males	210–215(2)	227–232(4)	—
Subcaudals			
females	112–118(4)	80+(2)	79(1)
males	114–123(2)	97–99(2)	—
Maxillary teeth	10±3	14–15+2–3	13–15+2–3
Frontal shield			
width: length	W<L	W<L	W<L
Anterior temporals			
lower: upper	L<U	L=U	L<U
Vertebral scales	normal	normal	enlarged

[1] Only two were examined. Data on three females and one male from Boulenger (1893).

The vertebral scales are markedly enlarged and truncate in one Bornean snake (FMNH 164746)[1] and less conspicuously enlarged in the second specimen (USNM 130244).[2] The vertebral scales do not differ from adjacent scales in the Philippine sample.

Granted that the Bornean and Philippine populations differ, how are these differences to be interpreted? Are these allopatric populations representatives of two distinct species or are they merely geographic races of a single species? One other species of *Stegonotus*, *S. dumerili*, occurs in the Philippine Islands. It differs from *muelleri* in subcaudal counts, in ventral counts, in number of scale rows on the neck, in maxillary tooth counts, and possibly in coloration (Table 3).[3] Thus *S. dumerili* differs from *S. muelleri*, with which it is sympatric, to about the same extent as the latter does from the Bornean snakes. I am, therefore, designating the Bornean population as a distinct spe-

[1] FMNH=Field Museum of Natural History.

[2] USNM=United States National Museum.

[3] Only small specimens of *dumerili* are known.

cies. But whether one refers to these snakes as separate species or as subspecies, the important fact is the greater similarity of the Philippine populations to one another than to the Bornean.

Stegonotus borneensis new species

Holotype.—Field Museum of Natural History no. 164746, a female collected at Nanga Tekalit, Kapit District, Third Division, Sarawak, on 24 May 1963, by Mr. F. Wayne King. Caught at night on gravel bar in small forest stream.

Paratype.—United States National Museum no. 130244, a female, from Bundu Tuhan, Mount Kina Balu, Ranau District, Sabah. Collected at 1,370 meters by Dr. D. H. Johnson.

Diagnosis.—A form of *Stegonotus* having enlarged vertebral scales, the upper anterior temporal scale twice as long as the one beneath it, uniform dark dorsal coloration, and each ventral transversely banded with black and white.

Description.—Head distinct from neck, flattened above; snout truncate, projecting slightly beyond lower jaw; diameter of eye shorter than eye-nostril distance; pupil vertically elliptical; body weakly compressed, with a noticeable vertebral ridge; belly flat, ventrals angulate laterally; vertebral scales distinctly wider than adjacent rows, twice as wide in holotype; anal plate single; tail 22 per cent of total length (in holotype).

Rostral broad, triangular, apex forming part of dorsal surface; internasals small, their suture one-fourth to one-third that of prefrontal suture; frontal wider than long, its length subequal to that of prefrontal; supraocular touching prefrontal, wider posteriorly where it equals one-half width of frontal; parietal twice as long as frontal; nasal semi-divided, its maximum depth one-half its length which is slightly greater than diameter of eye; loreal longer than deep; two preoculars, the lower twice as long as deep and less than half depth of upper one; upper preocular touching loreal; two postoculars, the lower equal to or smaller than upper; two enlarged temporals bordering the parietal, the anterior one shorter and narrower; the anterior enlarged temporal bordered below by two small temporals; nine upper labials, the fourth and fifth bordering the eye; upper labials subequal in length, increasing in depth to sixth and seventh which are deeper than eye; ten lower labials, the first five touching anterior chin shields; posterior chin shield shorter than anterior.

Tubercles on most dorsal and lateral head scales, scales of body smooth, without pits.

Scales in 21 rows on neck, reducing to 17 before level of twelfth ventral; third and fourth rows fuse to form 15 rows 76 to 86 ventrals anterior to vent; other counts and measurements given in Tables 1 and 2

Color in life (holotype) of head and body gray-black above and laterally, without markings; upper labials gray with pink bloom; chin gray with brownish bloom; ventrals light gray, each with blackish anterior band. In alcohol, both specimens dark brown; ventrals conspicuously barred.

ACKNOWLEDGMENTS

This work was partially supported by National Science Foundation grants G-6257 and G-20867. I am indebted to Dr. Alan E. Leviton for helpful criticism.

REFERENCES

BOULENGER, G. A.

1893. Catalogue of the snakes in the British Museum (Natural History). Brit. Mus. Nat. Hist., **1**, xiii +448 pp., 28 pls. London.

DUMÉRIL, A. M. C. and G. BIBRON

1854. Erpétologie générale ou histoire naturelle complete des reptiles. Vol. 7. Paris.

LEVITON, A. E.

1963. Remarks on the zoogeography of Philippine terrestrial snakes. Proc. Calif. Acad. Sci. (4), **31**, pp. 369–416.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 SEPTEMBER 19, 1967 No. 6

New Birds from Luzon, Philippine Islands

AUSTIN L. RAND
CHIEF CURATOR, ZOOLOGY. FIELD MUSEUM OF NATURAL HISTORY

AND

DIOSCORO S. RABOR
ASSOCIATE, BIRDS, FIELD MUSEUM OF NATURAL HISTORY

The following descriptions of novelties from the collections made by Dr. Rabor in extreme northwest, northeast, and south Luzon in 1959, 1960, and 1961 are published here in advance of the publication of a more comprehensive report on the zoogeography and geographical variations on Luzon. One new species and eight new subspecies are described.

Phoenicophaeus superciliosus cagayanensis new subspecies

Type.—Field Museum of Natural History no. 258851 from Luzon Island, Cagayan Province, San Pascual, Gonzaga (Mt. Cague in the Sierra Madre). Adult female, collected 18 April 1960 by D. S. Rabor.

Diagnosis.—Like *P. s. superciliosus* but differs in the much shorter red superciliary feathers; in the reduced amount of white at the bases of these red feathers; in the breast having a yellowish-green tinge (rather than a green tinge, present or absent); in having the white tips to the tail feathers smaller, and in averaging smaller in size.

Measurements.—*P. s. cagayanensis*, eight specimens, Cagayan Province: wing 143–152 (avg. 147 mm.); greatest length of red feathers of superciliary 11–15 mm. *P. s. superciliosus*, seven specimens from South Luzon: wing 149–163 (avg. 153.5 mm.); greatest length of red feathers of superciliaries 25–30 mm.

Range.—Known only from Cagayan Province, northeastern Luzon.

Library of Congress Catalog Card Number: 67–28268

No. 1029

Pycnonotus urostictus ilokensis new subspecies

Type.—Field Museum Natural History no. 253, 353, from Balaoi, Pagudpud, Ilocos Norte, Luzon Island, at 250 feet altitude. Adult male, collected 27 April 1959 by D. S. Rabor and R. B. Gonzales.

Diagnosis.—Like *P. u. urostictus* from central and southern Luzon and Samar but underparts with darker and more extensive brown; white tips to rectrices smaller, and bill larger, culmen male (7) 17–18 (avg. 17.6 mm.) against (8) 16–17 (avg. 16.5) for south Luzon birds.

Range.—Northern Luzon in Ilocos Norte and Cagayan Provinces; presumably intergrades with *urostictus* in central Luzon.

Brachypteryx montana andersoni new subspecies

Type.—Field Museum of Natural History no. 279302, from Mr. Isarog at Curry, Pili, Camarines Sur, southern Luzon, altitude 3,500–4,000 feet. Adult female collected 29 March 1961 by D. S. Rabor.

Diagnosis.—Like *B. m. poliogyna* from the highlands of northern Luzon but differs, in the female, in under tail-coverts being blackish to slate, at most tinged brownish (not rusty brown); crown being darker brown; and abdomen more slaty (less grey). Males like those of *poliogyna* but abdomen with less grey.

Measurements.—*B. m. poliogyna,* wing, ♂ (7) 65–68 (avg. 67 mm.), ♀ (5) 66–68 (avg. 66.8 mm.). *B. m. andersoni,* ♂ (4) 60–70 (avg. 67.3); ♀ (8) 65–70.5 (avg. 66.8 mm.).

Range.—Known only from Mt. Isarog, Camarines Sur, southern Luzon.

This is the first record of this mountain species from southern Luzon. The new race is named in honor of the late Mr. William Anderson, former Comptroller of Silliman University, who aided field work in former years.

Napothera sorsogonensis new species

Type.—Field Museum of Natural History no. 275745, from Mt. Bulusan, San Roque, Bulusan, Sorsogon Province, southern Luzon, altitude 800–1,000 feet. Adult female, collected 27 May 1961 by D. S. Rabor.

Diagnosis.—Similar to *N. rabori* but differs in having the crown olive much like the back (not reddish brown); in having the feathers of the back with narrow, indistinct, black edgings giving only a faint scaled pattern (not with a distinct scaled pattern); side of head dark grey to blackish, finely streaked or washed with white (not bright

reddish brown); chin and throat white with a narrow black malar line separated from the dark grey side of the head by a broader white stripe (not white generally spotted with black); sides of breast uniform grey, connected across upper breast by a narrow, uniform dark grey band; contrasting sharply with white on central part of lower breast and abdomen (not breast widely grey with a streaked and scaled pattern shading to grey-white of abdomen); wing slightly longer.

Measurements.—Three specimens taken the same place on the same day:

	Wing	Tail	Culmen	Tarsus
(a) type, female FMNH	88	72	25	32
(b) male (FMNH)	90	70	25	32
(c) male (Yale PM)	89	74	25	33

Soft parts.—Iris brown; bill, upper mandible blackish brown, lower half of lower mandible grey; feet light brown.

Range.—Known only from the type locality.

Remarks.—Despite the presentation of comparative data above, it seems advisable to present a description of the type in adult plumage and the other two in immature plumage.

Adult ? female plumage: Upperparts, forehead, and fore crown feathers greyish olive with faintly darker margins changing on central and hind crown to olive faintly edged darker; fore back olive, feathers with narrow, indistinct dark margins giving an obscure scaled pattern changing to uniform dark brown on lower back and paler brown on rump where the tips of the posterior feathers of the very dense rump feathers or "puff" are white giving a semi-concealed white bar; upper-tail coverts and upper surface of tail dark brown; upper greater and median wing-coverts black, broadly edged externally with brown and tipped with white; rest of upper-wing coverts greyish-olive brown, a few near the bend of the wing tipped with white; alula and primary coverts black tipped with white; remiges black broadly edged brown, the outer two sharply, the third indistinctly tipped with whitish on outer web.

Underparts: side of head dark grey to greyish black with a narrow white line from nostril to upper part of eye, a few white feathers above eye, ear covert region finely streaked white; chin and throat white, with a narrow black line extending from malar region to below ear coverts and separated from grey of side of head by a broader white band; sides of breast and side of neck uniform grey, joined across upper breast by a narrow dark grey band; flanks dark rusty brown;

lower breast and abdomen white, tinged rusty in region of vent; under-tail coverts dark red-brown; under surface of wing and tail fuscous.

Immature plumage: Crown olive brown; back and rump dark reddish brown, rump paler brown posteriorly and with tips of posterior feathers white to form a semi-concealed white bar; many of white markings in wing with a buffy to ochraceous wash; side of head dark grey to blackish, mottled with white on lower half.

Chin and upper throat whitish, some feathers obscurely tipped with dusky giving a mottled appearance; sides of breast and center of upper breast olive brown, flanks dull reddish brown; lower breast and abdomen dusky whitish grey.

Stachyris whiteheadi sorsogonensis new subspecies

Type.—Field Museum of Natural History no. 279301 from Mt. Bulusan, San Roque, Bulusan Municipality, Sorsogon Province, Luzon. Adult male collected 11 May 1961 by D. S. Rabor.

Diagnosis.—Like *S. w. whiteheadi* from northwestern Luzon but differs in the black edgings to the feathers of crown, superciliaries, and sides of face. Wing ♂ 65–71 (avg. 69 mm.).

Range.—Southern Luzon: Sorsogon and Camarines Sur Provinces, altitude 2,500–5,500 feet.

Phylloscopus cebuensis sorsogonensis new subspecies

Type.—Field Museum of Natural History no. 275,746, from Mt. Bulusan, San Roque, Bulusan, Sorsogon Province, Luzon, altitude 1,500–2,000 feet. Adult male, collected 4 May 1961 by D. S. Rabor.

Diagnosis.—Most like *P. c. cebuensis* from Negros Island but averages deeper yellow on chin, throat, and sides of head. Wing ♂ (10) 55–60 (avg. 57.4 mm.).

Range.—Southern Luzon in Camarines Sur and Sorsogon Provinces, altitude 300–3,500 feet.

It seems advisable to consider *cebuensis* a species with three races: *sorsogonensis*, yellowest race, southern Luzon; *cebuensis*, medium yellow, Negros; *luzonensis*, least yellow race, northern Luzon. *P. olivaceus* is thus left as monotypic.

Muscicapa herioti camarinensis new subspecies

Type.—Field Museum of Natural History no. 266, 335 from Mt. Isarog, Camarines Sur, Luzon. Male taken 26 April 1961 by D. S. Rabor.

Diagnosis.—Male has upperparts most like those of male *M. h. herioti* of northwestern Luzon but underparts quite different from those of that form and those of *M. h. enganensis* of northeastern Luzon in having throat pale ochraceous and upper breast buffy-rufous tinged with dusky (not throat and upper breast blue). Wing ♂ 77, 77; ♀ 75 mm.

Range.—Southern Luzon, known only from Mt. Isarog, Camarines Sur and Mt. Bulusan Sorsogon.

Sitta frontalis isarog new subspecies

Type.—Field Museum of Natural History no. 866, 562 from Mt. Isarog, at 3,500 feet altitude, Curry, Pili, Camarines Sur, Luzon. Adult male collected 28 March 1961 by D. S. Rabor.

Diagnosis.—Like *S. f. mesoleuca* of the western Cordellera of northwestern Luzon but differs in underparts being much deeper more cinnamon buff; in upperparts being deeper blue, and pale markings on nape and upper neck being reduced and more pinkish.

S. f. isarog differs from *S. f. aenochlamys* of Negros in underparts being duller; and in upperparts having reduced amount of pinkish on nape and neck. Wing ♂ (10) 74–79 (avg. 76.7 mm.).

Range.—Southern Luzon north to Manila area and thence north through the Sierra Madre (eastern Cordellera) to extreme northeastern Luzon; sea level to 4,000 feet at least.

Remarks.—The oft-quoted idea that this species showed altitudinal variation on Luzon was the result of comparing series of these two subspecies from different altitudes at widely separated localities.

Dicaeum hypoleucum cagayanensis new subspecies

Type.—Field Museum of Natural History no. 259,800 from Mt. Cagua, 2,000–3,000 feet, Gonzaga, Cagayan Province, Luzon. Adult male collected 30 April 1960 by D. S. Rabor

Diagnosis.—Male like that of *D. h. obscurum* of northwestern Luzon but still paler and less olive and yellow below, and with bill black, mandible black to base or with only a little dark brown at base. Wing (10) 53–56 (avg. 55.1 mm).

Range.—Northeastern Luzon in Cagayan Province.

FIELDIANA · ZOOLOGY

Published by
FIELD MUSEUM OF NATURAL HISTORY

Volume 51 | November 13, 1967 | No. 7

A Collection of Birds from the Ivory Coast

Melvin A. Traylor
Associate Curator, Birds, Field Museum of Natural History
and
Daniel Parelius
Abidjan, Ivory Coast

The avifauna of the Ivory Coast has been little studied, and therefore any opportunity to increase our knowledge is welcome. The collection of 339 birds that is the subject of the present report was made by the junior author in 1964 and 1965 while a student at the Lycée at Bouaké, Ivory Coast. Considering that he was never more appropriately armed than with a pellet gun, to which he was later able to add several mist nets, he made a collection that is surprisingly representative, containing 139 species of which 44 are new records for the country. In the following report, the field notes and general introduction are those of the junior author, and the taxonomic notes are those of the senior author.

The earliest report on birds of the Ivory Coast was that of Bouet and Millet-Horsin (1916–1917) who made two extended visits to the country, in 1906–07 and 1913–14. They evidently traveled widely for they include localities from the coast north to Korhogo. Although apparently they collected some specimens, the great majority of their records are based on sight records. The first proper collection was made in 1922 by Willoughby Lowe for the British Museum. He collected primarily in Béoumi and Bandama, localities not far west of Bouaké. Due to an unfortunate accident to his companion Hardy, Lowe's collecting was curtailed, but he managed to bring back some 345 specimens, representing 155 species. These were reported on by Bannerman (1923).

Between 1923 and 1960 there were only a few short papers on Ivory Coast birds. Dekeyser (1947a) recorded two species taken at Mt. Tonkoui in the mountainous west. M. Jean Brunel, an ardent amateur ornithologist, made a small collection around Abidjan which

Library of Congress Catalog Card Number: 67–28269

he sent to the Paris Museum where it was studied by Berlioz (1954). The following year, Brunel (1955) reported many of his own observations in the *Oiseau*. The only other major collection was made by Pfeffer and Chauvancy who in 1959–1960 spent three months collecting in the forest zone at Kpapekou and Mama. Their collection numbered 460 specimens of 120 species and was reported on by Pfeffer (1961).

Altogether, only 266 species are known from the Ivory Coast from actual specimens. To these may be added some 90 presumably valid sight records, but even 350 species is not much over half the total to be expected of a West African country with extensive forests and savanna. There is still a fertile field for ornithological exploration here.

General

The Republic of Ivory Coast, on the coast of the Gulf of Guinea, is a small, almost square-shaped country measuring about 300–400 miles on a side. It is bordered by (clockwise from the ocean) Liberia, Guinea, Mali, Upper Volta and Ghana. Ghana is the best studied of these, and the avifauna of the Ivory Coast does not differ strikingly from it. Comparing these two in size, we find that the Ivory Coast is wider, but does not reach quite so far to the north. The vegetational zones also follow much the same pattern as in Ghana; a little mangrove on the coast, a broad belt of rain forest extending inland for 100 to 200 miles, a horizontal strip of intergrading savanna and forest, and the true savanna farther to the north. Important differences are the mountainous forest in the west of the Ivory Coast, in the area of the Mt. Nimba range, and the existence in the northeastern corner of Ghana of a stretch of dryer savanna than is found in the Ivory Coast.

Climate follows the same pattern also as Ghana, with alternating rainy and dry seasons. In the extreme south there are two of each, the long rainy season occurring in late summer and autumn, the short one in late spring, and the long dry season occurring during the winter months, the short one between the two rainy seasons, about July and August. As one progresses toward the north these four seasons gradually merge into two, a rainy season in summer, and a dry season from about the end of November to April.

Aspects of the Avifauna

To date there are 266 species recorded from the Ivory Coast. According to the ranges given by Bannerman (1953), between 600

and 700 species will probably be found. Due to the several ecological, regions a number of species may be found to have two representative subspecies in the Ivory Coast.

In the following instances, the subspecies found in Ghana is different from that found in Liberia or Sierra Leone.

SPECIES	SUBSPECIES Ghana	Sierra Leone/Liberia
Francolinus bicalcaratus	*bicalcaratus*	*thornei*
Psittacus erithacus	*erithacus*	*timneh*
Tauraco persa	*persa*	*buffoni*
Tropicranus albocristatus	*macrourus*	*albocristatus*
Heliocorys modesta	*modesta*	*nigrita*
Phyllanthus atripennis	*haynesi*	*atripennis*
Trichastoma cleaveri	*cleaveri*	*johnsoni*
Baeopogon indicator	*togoensis*	*leucurus*
Diaphorophyia concreta	*concreta*	*lomaensis*
Turdus olivaceus	*saturatus*	*chiguancoides*
Cossypha albicapilla	*giffardi*	*albicapilla*
Hirundo senegalensis	*saturatior*	*senegalensis*
Nectarinia chloropygia	*chloropygia*	*kempi*
Cyanomitra cyanolaema	*octaviae*	*magnirostrata*
Estrilda astrild	*occidentalis*	*kempi*

Of these fifteen species, five have been found in the Ivory Coast. *Francolinus b. thornei* at Béoumi and Bouaké and *Turdus o. chiguancoides* at Bouaké prove to be the race of Liberia, but *Tauraco p. persa* at Béoumi and Kpapékou is the race of Ghana. The race of *Diaphorophyia concreta* at Mt. Tonkoui is still indeterminate. Dekeyser (1947a, p. 54) called it *harterti*, the race of Cameroon, but he had no material of any of the West African races and had to depend on written descriptions. There may actually be no difference between *concreta* and *lomaensis*, for the former is still known only from the faded type; White (1963, p. 32) unites them. Specimens of *Nectarinia chloropygia* from Bouaké and Abidjan are like those of Liberia and must be called *kempi*, but the extent to which they differ from Ghana birds is still not clear (see p. 110). The Ivory Coast, therefore, does seem to be a meeting ground for a few species with different races in Ghana and Liberia or Sierra Leone, but the total number of these species is small and they seem to have little zoogeographic significance.

Collecting Localities

Bouaké

Bouaké is a town of some 50,000 inhabitants in the center of the Ivory Coast. Vegetation is mostly savanna type; the land is composed of low, rolling hills, with a few scattered granite outcrops. There are no large rivers, and consequently few marshes of any size, but small streams are to be found almost in every valley; some dry up completely in the dry season (from November to March). Along these streams grows a surprising amount of gallery and fringing forest. A few large stands of primary forest occur, along with a great deal of secondary growth.

Abidjan

Abidjan is the capital and has a population of over 250,000. It is situated on the seacoast. All collecting was done in second growth near cultivated land. The humidity is always high. Rainy season is from April to June and August to October.

Korhogo

A large town in the north, Korhogo is in typical savanna country. It is interesting to note that nearly every village has a stand of primary growth nearby, which has been kept so for generations, and is used for "sacred forest" purposes, a mysterious part of tribal rites. This accounts for some of the birds of more sylvan habitat being found in the middle of the savanna. There are also a few gallery forests.

Doropo

A small village only nine kilometers from the Upper Volta border, Doropo is in a dry region in the Sudanese savanna. There are more scattered dwarf trees and acacia than at Korhogo.

Gazetteer

The various localities mentioned in the text are listed below. All are less than 2,000 ft. above sea level, and altitude plays no part in the distribution of birds in the Ivory Coast. Only in the region of Mt. Tonkoui in the west can montane birds be expected.

Abidjan	5° 21′ N; 4° 02′ W
Bavé	9° 34′ N; 4° 09′ W
Bondoukou	8° 03′ N; 2° 48′ W
Bongouanou	6° 39′ N; 4° 12′ W
Bouaké	7° 42′ N; 5° 02′ W
Bouna	9° 17′ N; 3° 00′ W

Boundiali	9° 32′ N; 6° 28′ W
Dabakala	8° 22′ N; 4° 20′ W
Doropo	9° 47′ N; 3° 20′ W
Ferkéssédougou	9° 36′ N; 5° 12′ W
Fétékro	7° 49′ N; 4° 42′ W
Foro-Foro	7° 59′ N; 5° 03′ W
Gouméré	7° 54′ N; 2° 59′ W
Groumania	7° 54′ N; 4° 00′ W
Katiola	8° 09′ N; 5° 06′ W
Kong	9° 09′ N; 4° 37′ W
Korhogo	9° 27′ N; 5° 39′ W
Laoudi-Ba	8° 18′ N; 2° 57′ W
Satama Sokoura	7° 54′ N; 4° 22′ W
Sinématiali	9° 35′ N; 5° 23′ W
Toumodi	6° 33′ N; 5° 01′ W
Varalé	9° 39′ N; 3° 17′ W
Wango-fitini	9° 24′ N; 4° 02′ W
Yaossédougou	8° 14′ N; 4° 14′ W

Acknowledgements

The junior author wishes to express thanks to Mr. Jean Brunel, Director of the Compagnie Agricole et Industrielle des Tabacs Africains, who took him on numerous field trips and whose ability and experience in identification aided him considerably; to Mr. Sopéna, Ingénieur de la Service des Eaux et Forêts, and others of the Bouaké Natural History Society; to the many missionaries who were helpful in various ways, particularly Rev. Lonnie Palmer of the Freewill, and Rev. Dennis Grudda and Rev. Donald Bigelow of the Conservative, Baptist Associations, who took time to help him procure specimens.

Also, to the senior author of this paper, without whose interest, encouragement and monthly communications over a period of more than two years I should not be writing this, I am more deeply indebted than I can say.

Finally, my thanks and appreciation go to my father, who was unfailingly encouraging and unselfishly devoted much of his free time to planning field trips and helping to carry out my projects, and my mother, who suffered me to keep live hawks and vipers in my bedroom, and unprepared specimens in her refrigerator!

The senior author would particularly like to express his appreciation to Mr. and Mrs. Rolf Parelius for the encouragement they gave their son in his natural history pursuits. This involved a consider-

able sacrifice of the peace and quiet of their home, which they cheerfully made.

SYSTEMATIC LIST

The order of families within the present list is that of Wetmore, while within the families the order of the species is that of Peters' Check-list for those families that have been covered, and of White's Revised Check-list for the others. Those species marked with an asterisk are here recorded for the first time from the Ivory Coast. Common and widespread species for which no new information is available are omitted from this list.

Butorides striatus atricapillus (Afzelius)

1 juv. ♂, 1 ♀, Korhogo, 8 June 1964.

A rather uncommon heron. Two nests in June were placed in fringing forest, in *Kassia* trees, about 20 ft. up and were made of twigs. One contained two eggs, and the other had three chicks.

The juvenal male has just begun post-juvenal molt, and the adult female is in complete post-nuptial molt.

Ardeola ibis ibis (Linnaeus)

2 ♀, Bouaké, 15 and 25 Nov. 1964.

These arrived in November and stayed during the dry season. They roosted in one large tree, and in the early morning before the cattle began to roam, many hunted insects for themselves.

***Scopus umbretta umbretta** Gmelin

1 unsexed, east of Bouaké, 17 Aug. 1964.

This specimen was a gift of Rev. L. Palmer.

This specimen with wing 320 mm. belongs to the larger nominate race, wing length (sexes combined) 280–333. The small race *minor*, wing 250–266, appears confined to the coastal mangroves from Sierra Leone to Nigeria; elsewhere in West Africa, inland from the coast, its place is taken by *umbretta* (*cf.* Dekeyser, 1947b, p. 372).

Accipiter tachiro macroscelides (Hartlaub)

1 ♂, Bouaké, 17 April 1965.

Specimen taken in a mist net in the undergrowth of primary forest near a marshy stream.

Although in adult plumage and already beginning molt into a second adult plumage, this bird still retains two worn juvenal secondaries. These must be 15–18 months old.

Butastur rufipennis (Sundevall)

1 ♀, Bavé, 1 Jan. 1965; 1 ♀, Dabakala, 25 Dec. 1964.

A common hawk in the northern regions; it only appeared at Bouaké at grass fires. Two captives were kept from January to June of 1965. Although Bannerman considers the species "absolutely mute" (1953, p. 282), and Chapin says also that it is "perfectly mute" (1932, p. 604), I recorded a loud cry of annoyance from the older of the two. Both captives were voluble when excessively handled, as might be expected. Within the confines of my room, I noticed a marked tendency on the part of the grasshopper buzzards and a black kite, *Milvus migrans*, to perch on the highest possible site. For both of the buzzards I had at first to cut raw meat into small chunks for them to eat. Whereas the older eventually took to tearing meat held beneath its feet, the younger did not; when I gave it a piece that was too large to swallow, it would take the piece out of its mouth with one foot, then seem at a loss as to what it should do. At first it would move sideways on the perch, looking very much confused, but soon learned to hold the foot up and peck the meat from between its toes.

Francolinus bicalcaratus thornei O.-Grant

1 ♀, Bouaké, 16 March 1964; 1 ♂, Bouaké, 1 May 1964.

This was by far the most common of the francolins in our area. It seemed to be just as common at Bouaké as farther north. It is a well-known game bird. Its harsh call is heard often in the early morning, though not so early as the Ahanta Francolin. Flocks of two to a dozen birds are commonly seen in the maize and igname fields. Although essentially a ground bird, it does not hesitate to perch on low branches, and I once saw one perched about 60 or 70 ft. up on a dead trunk of a tree. On another occasion one landed near me while I was standing in an igname field and moved about only a few feet away quite freely.

Although paler than typical *thornei* of Liberia, these specimens are nearer to that form than to the pale *bicalcaratus* of Ghana.

***Limnocorax flavirostris** (Swainson)

1 juv. ♂, Bouaké, 5 Feb. 1965.

The black crake was quite common in a stretch of marsh and cultivated land, and toward evening its queer gurglings and wheezes could be heard. The birds themselves were very shy and came out in the open only when assured that nothing was stirring. It was also to be found along the shady backwaters where vegetation enabled it

to hop from place to place. Once I saw several in open, marshy land that had just been turned over for planting. The birds were presumably getting earthworms and grubs from the soil. It usually flew only when surprised away from cover, at which time it flew heavily, with legs dangling, back to the reeds.

*__Neotis cafra denhami__ (Children)

1 ♀, Bondoukou, 19 Feb. 1965.

Gift of Rev. L. Palmer.

*__Actophilornis africana__ (Gmelin)

1 ♂, Foro-foro, 8 May 1965.

Treron calva sharpei (Reichenow)

1 ♀, Dabakala, 27 Dec. 1964.

Taken in wooded savanna.

The call of this pigeon begins with a clock-like "*tock-tock tock tock tock*," increasing in speed until a sudden switch is made to a whistled "*whooooo-eee-ooo-eee-ooo*," followed by a thrice-repeated grating note slightly reminiscent of the Bushfowl. The initial "tocking" is generally too soft to be detected in the field, unless at extremely close quarters. I heard it only because I kept three of these for awhile. These three established a peck order. Very often a "bout" would take place between two of them, the combatants striking *at* each other alternately, but not actually making contact.

*__Treron waalia__ (Meyer)

1 ♂, Kong, 1 Jan. 1965.

One of a band, taken in wooded savanna.

Streptopelia vinacea vinacea (Gmelin)

2 ♂, 1 ♀, 1 unsexed, Bouaké, Doropo, Bouna, 12 Feb. 1964, 18–31 Dec. 1964.

Common in the north, and present at Bouaké during the dry season.

*__Streptopelia senegalensis senegalensis__ (Linnaeus)

1 ♀, Korhogo, 16 June 1964; 1 ♂, Doropo, 31 Dec. 1964.

Common in the north; I never saw this tame dove near Bouaké.

Turtur afer kilimensis (Mearns)

2 ♂, 1 ♀, 1 unsexed, Bouaké, 23 May 1964–18 March 1965; 1 im. ♂, Abidjan, 23 June 1965.

Common but shy, and usually solitary.

Rand (1949) has written the most recent review of the West African races of *Turtur afer*. He accepted the pale nominate race from Senegal and Portuguese Guinea and the more richly colored *kilimensis*, extending west to Cameroon. The population of Liberia he separated as *liberiensis*, diagnosing this new race as darker than *afer*, and on the upper parts darker and less ruddy brown than *kilimensis*, it also averaged smaller than the other races, wing of male measuring in *afer*, 113–115 (114.2); in *kilimensis* from Cameroon 109–114 (111.2); and in *liberiensis*, 102–112 (106.2).

Our Ivory Coast specimens cannot be distinguished from recently collected Cameroon or East African specimens of *kilimensis*, and in size they are also comparable to that form, wing of males 111, 111, 114. Re-examination of Rand's Liberian specimens shows that the apparent color characters of *liberiensis* may have been due in part to post-mortem change. At the time of the original description, his Liberian material was very fresh, while the comparative material from Cameroon and East Africa was at least 20 years old. Sixteen years later the less ruddy tone of *liberiensis* is not so marked, particularly when compared to Cameroon material of comparable age. The size difference, of course, is not changed.

The juvenal male from Abidjan is undergoing a complete post-juvenal molt. Body molt is complete except for a few barred feathers on back and underparts, and wing molt has proceeded to the seventh primary, which is growing.

***Turtur abyssinica delicatula** (Sharpe)

1 ♀, Doropo, 29 Dec. 1964.

This specimen was with a male near a puddle where they had been drinking. There was an egg ready for laying in the oviduct.

Poicephalus senegalus versteri Finsch

1 ♂, Korhogo, 8 June 1964.

In flocks of about a dozen at Korhogo in June, and by couples at Doropo in December. I saw it eating the young buds of the *Kassia* tree at Korhogo.

Clamator levaillantii (Swainson)

1 ♂, Korhogo, 17 June 1964; 1 ♀, Bouaké, 21 Jan. 1965.

This species is rather rarer and more shy than the common coucal; it was more common at Korhogo than at Bouaké. I found it mostly in second growth.

Both specimens are in full molt, although one was taken in midwinter and the other in early summer. The Khorhogo male may belong to the southern population which breeds south of the Zambesi from October to March and winters in the equatorial regions.

Tyto alba affinis Blyth

2 ♀, 1 unsexed, Bouaké, 12 and 15 May 1964, 9 March 1965.

This was probably the most common owl at Bouaké. In June I saw five or six of them chasing and catching the flying termites that gathered under lights that lit our playing court. Since they are nocturnal, I doubt that they were in the habit of feeding on termites.

Stresemann (in Wolff-Metternich, 1956, p. 286) had a single female barn owl from Fernando Po. He was unable to distinguish it from mainland specimens and suggested that *poensis* Fraser (1843, Proc. Zool. Soc. London for 1842, p. 189) would prove to be an earlier name than *affinis* Blyth, 1862, for the barn owls of the whole of Africa. However, Amadon (1953, p. 418) who had two females from Fernando Po, found them darker below than mainland specimens and thought that *poensis* might be distinct from *affinis*. Rather than upset the well-established name *affinis* prematurely, we prefer to await more adequate series from Fernando Po.

*__Otus leucotis leucotis__ (Temminck)

1 ♂, Bouaké, 11 Feb. 1964; 1 ♀, Satama-Sokoura, 30 Nov. 1964.

The second most common owl. Its call was a rather soft, two-note *"kuh-cooo."*

*__Bubo africanus cinerascens__ Guérin

1 unsexed, Katiola, 1 Jan. 1965.

Ciccaba woodfordii nuchalis (Sharpe)

1 unsexed, Bongouanou, 13 Feb. 1965.

Gift of Mr. Le Clerc of the C.A.I.T.A.

*__Caprimulgus ruficollis ruficollis__ Temminck

1 unsexed, Katiola, 1 Jan. 1965.

Killed at night on a dirt road.

This species is evidently a rare but regular winter visitor to west Africa. Malzy (1962, p. 38) lists two recent records from Mali of birds taken in October, and one November record from Senegal. All of these were also nominate *ruficollis*.

***Caprimulgus inornatus inornatus** Heuglin

1 ♂, Bouaké, 19 May 1964.

This bird was taken in thick second growth with tangled, thorny vines, in the daytime. After being flushed, it landed and sat lengthwise on a branch.

***Apus affinis affinis** (Gray)

2 ♀, Bouaké, 9 Dec. 1964.

There was a small colony of 50–100 near us. Every morning they would fly out together and stay in a group for a few minutes screeching the while, after which they went their ways and hunted singly. The hottest hours they would spend in their nests, or at least in a group clinging to the nests, and come out again in the late afternoon.

Halcyon senegalensis fuscopilea Reichenow

1 ♂, 2 ♀, Bouaké, 4 Feb. and 30 May 1964.

By far the most common kingfisher at Bouaké.

The male, taken 4 February, has the crown about as dark as the darkest specimens of *senegalensis,* but the two females, one of them taken with the male, have the typical, sooty brown crown of *fuscopilea.* This mixture of pale and dark crowned birds may be due to southerly movements of the pale crowned birds during the dry season. All three birds are in the middle of wing molt, at approximately the same stage despite the difference in dates.

Halcyon malimbicus forbesi Sharpe

1 ♂, 1 ♀, Bouaké, 15 Jan. and 16 April 1965.

Much less common than *H. senegalensis*; never seen away from streams and gallery (or fringing) forest. It occurs in gallery forest as far north as Korhogo, although specimens were not obtained to determine the race.

Merops albicollis Vieillot

3 ♂, Bouaké, 29 March 1964, 6 and 29 March 1965.

Commonest and tamest of the bee-eaters at Bouaké, where it occurred during the dry season.

Friedmann (1930, p. 361) states that post-nuptial molt in this species in East Africa is irregular, some birds molting on their breeding grounds, July to September, and others on their wintering grounds, from October to March. In West Africa molt is definitely regular. Of some 40 birds taken from Sierra Leone to Cameroon during the

winter months, all show evidence of winter molt. Early October arrivals are in worn plumage, and the first primaries are replaced probably in November. Molt is prolonged, and a few birds taken in early May are still in full molt replacing outer primaries. The young birds also undergo a complete molt at the same time as the adults, but usually starting somewhat later, and it may be that those birds still in molt in May are in their first year.

As Friedmann noted, the situation in East Africa is not clear. However, on the basis of our material from Uganda and Kenya, it appears that those populations that breed locally and do not undergo a prolonged migration molt during the summer, July to September, while those that breed in the semi-arid zone further north, and migrate to East Africa for the winter, molt on their wintering grounds. We have both adults and juvenals in full molt taken in July and early August at Bugoma Forest, Uganda, and Elgeyu and Kendu Bay, Kenya, that must be locally breeding birds. On the other hand, from these and many other localities in East Africa we have numerous adults and young in full molt from October to March, and these are presumably wintering birds from farther north.

***Coracias abyssinica** Hermann

1 ♂, Gouméré, 27 Dec. 1964; 1 ♂, Bondoukou, 27 Dec. 1964; 1 ♀, Doropo, 30 Dec. 1964; 1 ♀, Bouaké, Feb. 1965.

Common in the north, but few wandered as far south as Bouaké. While riding from Bouaké to Dabakala late in December 1963, I was surprised to find one of these in the middle of the road, although it was about 8:00 P.M. A few miles later, another was found in that same position, but it was not so quick to get away as the first, and we hit it in the wing. The only time these birds assemble in any number is at the grass fires.

Tockus nasutus nasutus (Linnaeus)

1 ♂, Yaossédougou, 26 Dec. 1964; 1 ♀, Wango-fitini, 1 Jan. 1965.

The bird from Yaossédougou was taken in park savanna, as was the one from Wango-fitini, where the latter was attending a grass fire. They were common mostly in the North, and came down to Bouaké only during the dry season, never in any numbers.

***Lybius dubius** (Gmelin)

1 ♀, Bouaké, 8 Sept. 1964; 1 ♀, Doropo, 31 Dec. 1964.

This bird is more common in the North than at Bouaké. At Bouaké it was shot in second growth containing many *Ficus* bushes.

At Doropo and thereabouts it seemed to stay in the small groups of trees with dense undergrowth.

***Campethera nivosa** subsp.

1 ♂, Korhogo, 22 March 1965.

This specimen was taken in heavy gallery forest a few kilometers southwest of Korhogo. I heard it making a loud rattle, but did not manage to see it until I was right under it, and was impressed with its lack of fear. It perched across the branch, not along it, as most woodpeckers do.

This specimen has a remarkably long wing for this species, 98 mm., and, if typical of the population inhabiting the interior of the Ivory Coast, undoubtedly represents a new race. The maximum measurement given by Bannerman (1933, **3**, p. 431) for *C. n. nivosa* is 93 mm., based on 30 specimens, and the maximum for *efulensis* is only 91 mm., based on 19 specimens. Among our own material of 5 *nivosa* and 22 *efulensis*, none exceeds these measurements.

Mesopicos goertae agmen Bates

1 ♂, Bouaké, 28 Aug. 1964.

Collected in a tree on a savanna hillside.

Mirafra rufocinnamomea buckleyi (Shelley)

1 unsexed, Bouaké, 15 Sept. 1964.

This is one of the clapper larks with a characteristic flight pattern as described by Bannerman (1953, p. 808) and with a characteristic sound, i.e., "*prrrrp-prrrrp prrrrrrp*," the third being the longest. Many times it can be heard in the sky flying so high that it is out of sight. They also are one of the first birds to waken in the morning, and it is startling to have one drum nearby on a misty morning at dawn.

Mirafra nigricans erythropygia Strickland

1 ♀, Fetekro, 17 Jan. 1965.

This bird was taken while perching high in a bare-branched tree in park savanna.

Hirundo rustica rustica Linnaeus

1 ♂, 3 ♀, 1 unsexed, Bouaké, 14 Sept.–10 April, 1964 and 1965.

Often seen in large companies in fall and spring.

The earliest sign of molt is in an immature male taken 28 September which has shed its first primaries. An immature female taken

12 November is growing its first two primaries, while a female taken 10 April is in fine, fresh plumage.

***Hirundo lucida lucida** Verreaux

1 ♀, Ferké, 5 Aug. 1964.

This one was taken in savanna, in a town where it was sitting on a wire with several others. It has begun post-nuptial molt, with the third primary growing in.

***Hirundo leucosoma** Swainson

1 ♂, Bouaké, 9 June 1965.

In June of 1964 I found a nest of this species placed about 15 ft. down in a well. Next month there was a new nest, about 20 ft. up, in a water tower right beside the well, and it might have been the same pair that built the two, for I never saw more than two birds at a time. The young birds excreted waste over the edge of the nest. At night one of the adult birds covered the young, even when they were quite well grown.

***Hirundo abyssinica puella** Temminck and Schlegel

1 ♂, 1 ♀, Bouaké, 4 May 1965; 1 ♂, Korhogo, 11 June 1964.

These were commonly seen on wires over streams, in savanna. The specimen from Korhogo was carrying mud for its nest. Nests at Bouaké were in small colonies under culverts.

***Dicrurus ludwigii sharpei** Oustalet

1 ♀, Bouaké, 16 May 1965.

Conspicuous and common only in a small stand of primary forest near Bouaké. Their song is much more musical and loud than that of *D. adsimilis*. They cannot stay in the forest canopy all the time, for one was caught in a mist net in thick undergrowth just a few feet from the ground.

Dicrurus adsimilis divaricatus (Lichtenstein)

1 ♂, Bouaké, 30 Sept. 1964.

This species was definitely more common at Korhogo and Doropo than at Bouaké.

Dicrurus adsimilis atactus Oberholser

1 ♀, Abidjan, 18 June 1965.

The race *atactus* with darker, less glossy, back is evidently confined to the coastal forests of the Ivory Coast, and its place in the interior savanna is taken by the widespread *divaricatus.*

***Corvus albus** Müller

1 ♂, Laoudi-Ba, 28 Dec. 1964.

Common and much associated with man.

***Turdoides plebeja platycircus** Swainson

1 im. ♂, Korhogo, 6 June 1964.

This babbler was not recorded at Bouaké, although it was common in little parties at both Korhogo and Doropo.

This specimen is in post-juvenal molt, and breeding must have begun before the rains.

Andropadus virens erythopterus Hartlaub

4 ♂, 2 ♀, Bouaké, 15 Jan.–18 April 1965; 2 ♂, Abidjan, 19 and 21 June 1965.

One of the most common birds of secondary forest, where it is much more frequently heard than seen. So well does it escape detection that I recognized its call for eight months before seeing one.

***Andropadus latirostris congener** Reichenow

1 ♂, Abidjan, 22 June 1965.

Taken in heavy undergrowth, secondary bush.

***Chlorocichla flavicollis flavicollis** (Swainson)

1 ♂, Sinématiali, 23 March 1965.

Taken in a large tree in gallery forest. It was with a small band of the same species.

Phyllastrephus scandens scandens Swainson

1 unsexed, Bouaké, 16 May 1965; 1 ♀, Korhogo, 13 June 1964.

Although Bannerman says that it is not found in dense undergrowth, it was seen there more often than not. At Gawi on the Comoé River, in the savanna of the Bouna Reserve, it was extremely common. Its call is a peculiarly liquid babbling. They move around the forest in small bands, sometimes following single file.

Nicator chloris (Valenciennes)

1 juv., 1 ♀, Abidjan, 21 June 1965.

Saxicola rubetra Linnaeus

2 ♂, 4 ♀, Bouaké, 2 Nov. 1964–31 Jan. 1965.

A common migrant which appears during the long dry season. It is often to be seen perched on telegraph wires, from which it sallies

forth after insects. Although it rarely sings, at times I have heard a soft but beautiful song from this bird. It also has a metallic note, like a buzz mixed with a chirp, which is heard more often.

Although the whinchat does not, as a rule, molt its flight feathers on its wintering grounds, one female, taken 12 January and marked "skull not ossified," has replaced the first primaries.

***Turdus olivaceus chiguancoides** Seebohm

1 ♂, Doropo, 30 Dec. 1964; 1 ♂, 1 ♀, Bouaké, 22 May 1964 and 5 March 1965; 1 juv. ♀, Bouaké, 28 Sept. 1964; 1 ♀, Korhogo, 11 June 1964.

The Kurrichane thrush is not uncommon at Bouaké, where it seemed to favor gardens with plenty of vegetation. Its song is heard mostly in the early rains, at which times it perches rather conspicuously atop some tree. It has sweet notes, never repeated more than three times, which it sings incessantly with a great deal of variation in pattern.

The young bird from Bouaké has just begun post-juvenal molt.

***Acrocephalus arundinaceus arundinaceus** (Linnaeus)

1 ♂, 1 ♀, Bouaké, 5 Feb. and 30 April 1965.

These specimens were taken in rank marsh reeds, where this warbler seemed to be almost the only species of bird.

Cisticola erythrops erythrops (Hartlaub)

1 unsexed, Bouaké, 15 Feb. 1964; 1 ♂, 1 ♀, Abidjan, 21 and 23 June 1965.

Cisticola lateralis subsp.

1 ♂, 1 ♀, Bouaké, 15 March 1964, 9 April 1965; 1 juv. unsexed, Bouaké, 21 Sept. 1964.

I agree with Rand (1951, p. 625) that the population of Cameroon can hardly be included in nominate *lateralis*. Rand had seven specimens from Cameroon that could be separated at a glance from nine topotypes of *lateralis* from Liberia, the latter being much darker and more sooty on the upper parts. We now have some 15 additional specimens from Cameroon, and they, too, can be told at a glance from the Liberian birds. Cameroon should be included in the range of the browner race *antinorii* of East Africa.

The two Bouaké adults are similar to Cameroon birds rather than to those of adjoining Liberia. However, until material from Ghana

and Nigeria is examined, and better series are forthcoming from the Ivory Coast, it would be rash to extend *antinorii* so far west.

***Cisticola natalensis strangei** (Fraser)

2 ♂, 1 unsexed, Bouaké, 19 Sept. 1964–6 June 1965.

Due to mistrust of my field identifications, I hesitate to note any observations about these grass-warblers.

***Prinia erythroptera erythroptera** (Jardine)

2 ♀, 1 unsexed, Bouaké, 27 Aug.–18 Dec. 1964.

This warbler is usually quite conspicuous, with a considerable variety of notes. Generally, two or three are found together, and they seemed at Bouaké to prefer a thick, grassy habitat with small bushes. However, I once collected one from the branches of a large tree some 40–50 ft. up.

This is a short, westerly extension of range for this species, which previously has been taken only west to Ghana. We agree with White (1962a, p. 688) that *Heliolais* should be submerged in *Prinia*.

***Prinia subflava** subsp.

1 unsexed, Bouaké, 25 Aug. 1964; 1 juv. ♂, Bouaké, 18 Dec. 1964.

The unsexed adult, taken 25 August, is in breeding plumage with black bill and cannot be distinguished from the perennially-plumaged *melanorhyncha*. On the other hand, the juvenal male is molting into a first winter dress that is similar to the winter dress of nominate *subflava*. If this first winter dress is similar to that of the adult, then the population of Bouaké must be included in *subflava*, which shows marked differences between the darker, grayer breeding plumage and the paler, browner winter plumage.

***Hypergerus atriceps** (Lesson)

2 ♂, Bouaké, 25 April 1964, 16 May 1965.

This bird seems to be among the more shy species. I found it usually in undergrowth of either primary or secondary forest, although it does not hesitate to fly in the open from place to place. It has a rather harsh note, and also a song which it gives from a tree and repeats over and over to the point of monotony, a whistled "*wheee-oooo.*" It was usually in pairs, at least in the early rains.

Camaroptera superciliaris willoughbyi Bannerman

1 ♂, Bouaké, 19 March 1965.

Taken in thick secondary forest; an uncommon species.

Amadon (1953, p. 424) doubts the validity of *willoughbyi* and White (1962a, p. 712) recognizes no races. However, our specimen shows clearly the characters ascribed to *willoughbyi*. Compared to *flavigularis* it is brighter green above and more nearly white below. On the other hand, it would be difficult to separate it from some of the more brightly colored specimens of *pulchra* from northern Angola.

***Camaroptera chloronota kelsalli** Sclater

1 ♀, Abidjan, 21 June 1965.

Taken in dense undergrowth.

Camaroptera brachyura tincta (Cassin)

2♂, 1 unsexed, Bouaké, 14 Jan.–25 May 1965.

Probably the most common warbler, it usually stays in the undergrowth of forests. In May one was chasing another through the trees and bushes of some primary forest with great abandon and vocalization.

***Sylvietta denti hardyi** Bannerman

1♂, Abidjan, 20 June 1965.

Taken in thorny thicket.

Hylia prasina prasina (Cassin)

2♂, 1 ♀, Bouaké, 3 Feb.–22 May 1965.

White (1962a, p. 738) calls the populations from Portuguese Guinea to Ghana *superciliaris*, characterizing them as darker above and below than the nominate form. When the Ivory Coast birds are compared to a series of fresh topotypical *prasina* from Gabon, there are no evident differences, and the former must be placed in *prasina*.

Diaphorophyia blissetti Sharpe

2 ♀, Abidjan, 24 June 1965.

These two were taken in dense second growth, near an area of cultivated land.

Serle (1957, p. 641) reports collecting *blissetti* and *chalybea* within a few miles of one another in the Kumba division of Cameroon, with no evidence of intergradation. We agree with him that they should be maintained as separate species.

Terpsiphone viridis ferreti (Guerin)

1♂, Bouaké, 12 Feb. 1965.

Found occasionally in the tall trees of gallery forest at Bouaké.

In a gallery forest at Sinématiali, near Korhogo in the north, it seemed quite common.

This male is in the white phase, with back and tail wholly white except for a few black shaft streaks. This is by far the most common plumage phase in the Ivory Coast, and is characteristic of *ferreti*, which ranges across the Sudanese savanna from the Ivory Coast and Mali to Abyssinia. The white phase of *speciosa* of Lower Guinea is similar, but the outer rectrices are almost invariably black. White (1963, p. 40) was the first to recognize that *ferreti* reached the Ivory Coast.

***Macronyx croceus croceus** (Vieillot)

2 ♀, Bouaké, 1 Sept. and 24 Dec. 1964.

This is a common bird and more conspicuous than most pipits because of its size and coloring. It is often flushed up from areas of short or no grass, and is usually seen in pairs, which are very devoted to each other. It has a characteristic flight, flapping and gliding with down-curved wings, and uttering its two-note call. It also has a rather pretty song. It perches often on small bushes, where its feet have difficulty gripping the perch, as evidenced by the constant jerking and seeming loss of balance.

Tchagra senegala senegala Neumann

1 ♂, Doropo, 30 Dec. 1964; 1 ♀, Boundiali, 20 June 1964.

The specimen from Boundiali was taken in rather open bush. This species is often heard singing, but is not at all conspicuous. During courtship it also has a variety of buzzes and clicks, uttered while flying up and down to impress the females.

The Ivory Coast birds cannot be separated from topotypical *senegala*. White (1962b, p. 22) is probably correct in considering *pallida* of Ghana to be a synonym of *senegala*.

***Laniarius ferrugineus major** (Hartlaub)

2 ♂, Bouaké, 8 Sept. 1964 and 12 March 1965.

A well-known songster, this bird is found in secondary forest, the thicker the better, where its secretive movements recalled the coucal.

***Corvinella corvina togoensis** Hartlaub

1 ♀, Doropo, 31 Dec. 1964.

Always gregarious and local at Bouaké and at Korhogo and Doropo. We follow White (1962b, p. 39) in using *togoensis* for Ivory Coast birds.

***Lamprotornis chalcurus chalcurus** Nordmann

1 unsexed, Varalé, 28 Dec. 1964.

Taken from a flock of some two score in kapok trees in open country. Varalé is just a little south of Doropo.

This specimen is aberrant in color, lacking the rich violet color on the tail that is characteristic of typical *chalcurus*, and actually appearing more like the closely similar *chalybeus* which has a green tail. However, in other characters, particularly its short tail, it is typical *chalcurus*. Tail lengths of the two species are:

	♂♂	♀♀
chalcurus	71 – 80	70 – 75
chalybeus	85 – 92	80 – 85

The unsexed Varalé bird has a tail length of 74, within the limits of *chalcurus*, but smaller than even the smallest female *chalybeus*. In both species the ear coverts are dark blue, but those of *chalcurus* are darker and more sharply defined from the green head than those of *chalybeus*. In this character, also, the Varalé bird is *chalcurus*.

***Nectarinia venusta venusta** (Shaw and Nodder)

1 ♂, Bouaké, 10 Nov. 1964.

This specimen is most peculiar. The iridescent green upperparts, when viewed directly from above, have a pinkish coppery wash that I am unable to find in any other specimen. Presumably, this is a mutant structural defect, for the pigmented areas of the bird are typical of nominate *venusta*.

Nectarinia chloropygia kempi (O.-Grant)

1 ♂, Bouaké, 22 April 1965; 1 ♂, Abidjan, 19 June 1965.

Usually seen in second growth vegetation, where it is attracted by flowers of various kinds. Exceedingly common at Abidjan—in fact, it was the only sunbird I recognized there.

Our few specimens of *chloropygia* from West Africa do not correspond with the arrangement of subspecies of either Bannerman (1948, p. 186) or of Serle (1956, p. 104) and White (1963, p. 75). Bannerman recognizes four races: from Sierra Leone to the Ivory Coast, birds are pale olive below (*kempi*); from Ghana through southern Nigeria they are darker (*chloropygia*); from southern Cameroon and eastward they are darker still (*luhderi*); while on Fernando Po and Cameroon Mt. they are similar in color to *chloropygia* but larger (*insularis*). Serle and White recognize only two races: dark birds from east of the Niger River through Cameroon (*chloropygia*, with *luhderi* and

insularis as synonyms); and pale birds from west of the Niger to Sierra Leone (*kempi*).

Our material consists of a long series of the dark-bellied "*luhderi*" from southern Cameroon, single specimens from Mt. Cameroon, Ifon in southwestern Nigeria, and Liberia, and the two males from the Ivory Coast. Contrary to the above authors, the Mt. Cameroon and Ifon birds are much paler below than even the *kempi* from the Ivory Coast and Liberia. The Mt. Cameroon specimen in particular could not possibly be associated with the dark southern Cameroon birds where Serle and White would place it. Serle has pointed out that wear causes considerable variation in color in the underparts, but the darkness of our Ivory Coast and Liberian *kempi* compared to Nigerian birds cannot be correlated with wear since all specimens are in immaculate fresh plumage and the Bouaké bird is just completing molt. While we cannot possibly revise the races of *chloropygia* on the meager material available, neither of the arrangements above seems satisfactory.

Nectarinia coccinigaster (Latham)

3♂, 3♀, Bouaké, 15 Feb. 1964–10 Feb. 1965.

Probably the commonest savanna sunbird in the Bouaké area.

Nectarinia superbus ashantiensis (Bannerman)

1 im. ♂, Bouaké, 21 May 1964.

***Zosterops senegalensis senegalensis** (Linnaeus)

2♂, Bouaké, 15 Feb. 1964 and 18 March 1965.

The white-eye is a rather tame little bird, often seen in gardens, usually in small parties, which search the branches for insect food. They keep in touch with each other with little twittering cries.

These Bouaké birds are typical of the paler, more yellowish nominate race of the savannas of West Africa. If the darker, more olive, *demeryi* is found in the Ivory Coast, it must be closely confined to the forest areas.

Ploceus nigerrimus castaneofuscus Lesson

2♂, Bouaké, 20 Oct. 1964.

These weavers nest in heavy elephant grass during the latter part of the rains. On October 20, when the two specimens were collected, there was a good-sized colony of some 40 nests at the base of a small granite outcrop. The males displayed by hanging beneath the nest with fluttering wings, and giving forth a waterfall of wheezes and

whistles. I found spaces, below the nests which I inspected, that were clear of any grass stems except the ones supporting the nest. The ground also was clear of debris, and there were often small piles of white-flower petals. The grass could have been used to construct the nests, although most of the males seem to fly away to other places to get the material. The eggs had not been laid in the nests I checked.

Earlier this same group of weavers had built nests in a different area a hundred yards away, but had never laid in them.

Ploceus superciliosus (Shelley)

2♂, 1♀, 1 unsexed, Bouaké, 22 March 1964–6 June 1965.

This weaver is rather common around Bouaké, although I did not find it anywhere else. It lives in small groups of six to ten individuals, generally in thick elephant grass.

Malimbus nitens (Gray)

1♂, Bouaké, 3 June 1964; 1♀, Groumania, 27 Dec. 1964.

At Bouaké, this species was found only in a stand of primary forest ten miles to the east. The first specimen was taken from a group, and empty nests were found suspended over the pools of water, presumably of this species. The second specimen from Groumania was a solitary bird in partially cultivated land bordering primary growth.

***Quelea erythrops** (Hartlaub)

4♂, 1♀, 1 unsexed, Bouaké, 16 Dec. 1964–14 March 1965.

Often found in mixed flocks with other weavers in the off season, but not very numerous at Bouaké.

***Vidua nigeriae** (Alexander)

1♂, Bouaké, 28 Aug. 1964.

This bird was shot while with some females and apparently other males in a manioc field that was under preparation. It was uncommon at Bouaké, although other little Indigo finches (I could not be sure of which species) were commonly seen around villages in the north.

***Pyrenestes sanguineus sanguineus** Swainson

3♀, 1 juv. ♀, Bouaké, 17 April–2 June 1965.

Several of these were taken in gallery forest directly bordered by a reedy swamp, which opened into a thick marsh a few yards downstream.

The finding of *P. s. sanguineus* in the Ivory Coast was the most interesting discovery made by Parelius. Prior to this it had been known only from Senegambia and Portuguese Guinea where it is extremely rare. The only other record since 1909, when Ansorge took his specimen at Gunnal, are two sight records by Cawkell (1960, p. 137) on the Gambia River. Nominate *sanguineus* is distinguished from *coccineus*, the race of Sierra Leone and Liberia, by its broader bill and longer wing. Measurements of the two races, from Chapin (1924), are given below, compared to those of our three adult females from Bouaké.

		wing length	bill width
sanguineus	8 ♂	69–74.5 (72)	17.5–20 (18.2)
	1 ♀	70.5	18
coccineus	17 ♂	60–63 (61.7)	11.9–14.4 (12.8)
	15 ♀	57–63 (60.9)	12–15 (12.6)
Ivory Coast	3 ♀	67, 70, 72	13.8, 18.4, 19.1

It will be noted that one bird, with bill width 13.8, is in the size range of *coccineus*, but in wing length it is nearer to *sanguineus*. This is the first time that such variability in bill width has been noted within any one population of the species *sanguineus*, but it is found commonly in the related species *ostrinus*. Chapin (1954, p. 490) has shown that in *ostrinus* the race with the largest bill, *maxima* (=*frommi*), is characteristic of gallery forest in the savanna, that the medium-billed race *ostrinus* is found around the edge of the tropical forest, and that the smallest race *rothschildi* is found in clearings of the forest. He suggests that the present occurrence of large- and small-billed birds together is due to the rapid change in habitat occasioned by the agricultural activities of man. He also suggests that the broad-billed *sanguineus* is the savanna representative of the small-billed, forest *coccineus*. This is borne out by our material, for Bouaké is in an area of savanna with gallery forest; this population may prove to be continuous with those of Gambia and Portuguese Guinea when the drier interior of Guinea is better known.

The relationship of *sanguineus* and *ostrinus* is obviously close, and White (1963, p. 180) unites them in a single species. The clue to this relationship will be found in the Ivory Coast, but at present the evidence is equivocal. Berlioz (1954, p. 661) reported a female of *P. o. ostrinus* from Bingerville, near Abidjan, with a mandibular width of 15 mm. Unfortunately, there is no way to distinguish between the females of *P. o. ostrinus* and *P. s. coccineus*, so this record is open to

question. However, the following year Brunel (1955, p. 16) reported that Africans had brought him nests and adult males and females of both *ostrinus* and *coccineus*. Unfortunately, only the single female reported by Berlioz was preserved, but the male of *ostrinus* with its black upperparts is unmistakable, and this species certainly reaches the Ivory Coast. However, the male of *coccineus* could easily be confused with females of either species, since all have brown backs, and the presence of both species at Bingerville is still not certain. The same question might be raised about the Bouaké females, whether they might not be *P. o. frommi*, the large-billed race of *ostrinus*, which has been found as far west as Togo. There is no way to separate the females of the two, but both Parelius and Brunel have observed or handled several other specimens at Bouaké besides those preserved, and as none of them showed the black back of *ostrinus*, it may be assumed that they were all *sanguineus*. The solution to the problem, whether or not *ostrinus* and *coccineus* meet and behave as good species, must await more extensive observations and collections in the Ivory Coast.

***Estrilda bengala bengala** (Linnaeus)

1 ♀, Korhogo, 15 June 1964

Extremely common at Korhogo, where it was apparently breeding in June. The male would sit on a branch with a small piece of grass in his beak, singing prettily for the female, who, however, showed little or no interest.

***Estrilda senegala senegala** (Linnaeus)

2 ♂, Bouaké, 5 Dec. 1964 and 28 Jan. 1965.

This common little firefinch is usually seen in the vicinity of human habitations. They often gather in spots where water is thrown out, or where grain is threshed. They seemed to be somewhat more common in the north than at Bouaké.

***Estrilda rubricata polionota** (Shelley)

1 ♂, 1 unsexed, Bouaké, 11 Jan. and 5 March 1965.

The areas where grass is invading secondary growth is a favorite place of this bird. It is quite shy, and usually found in pairs. They never seem to fly higher than necessary to skim over the ground or the grass and settle down farther away, giving a few characteristic notes in flight. Like other firefinches, they do most of their feeding on the ground.

***Ortygospiza atricollis ansorgei** O.-Grant

1 ♂, 1 ♀, 3 unsexed, Bouaké, 14 Nov. 1964–2 May 1965.

This is a common little bird with a characteristic but hard-to-describe call which it utters when flushed, as it flies jerkily to land a few yards away. It is often seen along the side of dirt roads in pairs or threesomes, and also in small groups of four to six individuals in cultivated land bordering a stream. It is usually found where the soil is of a grayish color, with considerable clay content.

In a recent revision (Traylor, 1963, p. 141) of *O. atricollis*, I stated that one character by which males of *atricollis* could always be distinguished from males of the related *gabonensis* was the blackish or horn-colored upper mandible. In male *gabonensis* the upper mandible is always red. Contrary statements about *atricollis* I considered as probably due to confusion with *gabonensis*. However, in their new monograph of the waxbills, Immelmann *et al.* (1963–1965, pp. xiii and 369) state that the upper mandible of *atricollis* becomes red during the breeding season. Our fresh material from the Ivory Coast, plus information from several observers in Africa, show that Immelmann *et al.* are correct, and that at least in the majority of races the male of *atricollis* does have a red upper mandible during the breeding season.

The two adult males of *O. a. ansorgei* from Bouaké have the upper mandible bright red, similar in color to the lower mandible. Mr. P. A. Clancey writes me that in the race *muelleri* of Natal, the whole bill is also red during the breeding season. Mr. M. P. Stuart Irwin says (*in litt.*) that the same is true in *muelleri* of Zambia and Rhodesia, and in *pallida* of Bechuanaland. Unfortunately, he had no breeding material of *muelleri* or *smithersi* taken in the areas of sympatry with *gabonensis* in Zambia. However, his description of *smithersi* taken in October, about two months before breeding, suggests that even this race may assume a red bill, "5 ♂♂: coll. 9, 10, 11th October have the maxilla much less dark [than August birds], though they are a bit variable, but obviously at this juncture it would seem to have been taking on a reddish suffusion." The case of *O. a. ugandae*, which is sympatric with *O. g. dorsostriata*, produces the only positive contrary evidence. Chapin (1954, p. 499) collected a series of *ugandae* at Kasenyi on the shores of Lake Albert in September, at which time they were breeding and one female was about ready to lay. He gives the bill color of male *ugandae* as "very dark crimson, washed with blackish on mandible," while bill color of the sympatric *dorsostriata*, taken at Bogoro in the same month, was "rather dull scarlet."

If, as one would normally expect, different bill colors would serve as species recognition marks between the otherwise closely similar *atricollis* and *gabonensis*, it would be unexpected to find that the bills become alike during the breeding season when this recognition mark would be most useful. It does appear that this may be the case with *smithersi*, although the evidence is not conclusive, but is apparently not the case with *ugandae*. Outside of the areas of sympatry, however, it is apparent that *atricollis* races do acquire a wholly red bill during the breeding season, contrary to my previous statement.

Lonchura cucullatus cucullatus (Swainson)

2♂, Bouaké, 31 May 1964 and 5 March 1965.

One of the commonest of the estrildines at Bouaké, where it was always to be seen in the bougainvillae on our porches. It was difficult to tell when it was breeding, because of the communal nests they build to roost in. However, I did discover one nest in May, that contained several eggs. It was built in a small leafless tree, about 5 ft. up, and there was a wasp nest beside it, to my misfortune.

Serinus mozambicus caniceps (d'Orbigny)

2♂, 2♀, 1 unsexed, Bouaké, 23 April 1964–3 June 1965.

A common little bird of park woodland and, more often, clearings of man. I have twice seen flocks of this species hawking for insects from small trees.

REFERENCES

AMADON, D.

1953. Avian systematics and evolution in the Gulf of Guinea. Bull. Am. Mus. Nat. Hist., **100**, pp. 393–452.

BANNERMAN, D. A.

1923. Report on the birds collected during the British Museum Expedition to the Ivory Coast (French West Africa). Ibis, pp. 667–748.

1933. The Birds of Tropical West Africa, **3**, xxxv+487 pp. London.

1948. The Birds of Tropical West Africa, **6**, xxxix+364 pp. London.

1953. The Birds of West and Equatorial Africa, 2 vols., xiii+1526 pp. London.

BERLIOZ, J.

1954. Étude d'une petite collection d'Oiseaux de Cote d'Ivoire. Bull. Mus. Nat. Hist. Nat., Paris (2), **26**. pp. 657–662.

BOUET and MILLET-HORSIN

1916–1917. Liste des oiseaux recueillis ou observés a la Cote d'Ivoire en 1906–1907 et en 1913–1914. Rev. Fr. Orn., **4**, pp. 345–349, 371–375; **5**, pp. 3–6.

BRUNEL, J.

1955. Observations sur les oiseaux de la basse Cote d'Ivoire. Oiseaux, **25**, pp. 1–16.

CAWKELL, E. M.
1960. Notes from the Gambia. Ibis, **102**, pp. 136–137.

CHAPIN, J. P.
1924. Size variation in *Pyrenestes*, a genus of weaver-finches. Bull. Am. Mus. Nat. Hist., **49**, pp. 415–441.
1932. The birds of the Belgian Congo, 1. Bull. Am. Mus. Nat. Hist., **65**: x+756 pp.
1954. The birds of the Belgian Congo, 4. Bull. Am. Mus. Nat. Hist., **75B**, ix+846 pp.

DEKEYSER, P. L.
1947a. Notes sur quelques oiseaux peu communs de l'A. O. F. Bull. Mus. Nat. Hist. Nat., Paris (2), **19**, pp. 54–56.
1947b. Notes d'Ornithologie Ouest Africaine. Bull. Inst. Fr. Afr. Noire, Dakar, **9**, pp. 358–382.

FRIEDMANN, H.
1930. Birds collected by the Childs Frick expedition to Ethiopia and Kenya Colony. Part 1. Non-passeres. Bull. U. S. Nat. Mus., **153**, 516 pp.

IMMELMANN, K., J. STEINBACHER and H. E. WOLTERS
1963–1965. Prachtfinken, 2nd ed., **1**: xv+427 pp. *in* Steinbacher and Wolters, eds. Vögel in Käfig und Voliere. Aachen.

MALZY, P.
1962. La Faune Avienne du Mali. Oiseau, **32**, no. spécial, 81 pp.

PFEFFER, P.
1961. Étude d'une collection d'oiseaux de Cote d'Ivoire. Bull. Mus. Nat. Hist. Nat., Paris (2), **33**, pp. 357–368, 451–461.

RAND, A. L.
1949. The races of the African Wood Dove *Turtur afer*. Fieldiana: Zool., **31**, pp. 307–312.
1951. Birds from Liberia. Fieldiana: Zool., **32**, pp. 561–653.

SERLE, W.
1956. Taxonomic notes on *Cinnyris chloropygius* (Jardine). Bull. Brit. Orn. Club, **76**, pp. 104–105.
1957. A contribution to the ornithology of the eastern region of Nigeria. Ibis, **99**, pp. 371–418, 628–685.

TRAYLOR, M. A.
1963. Revision of the Quail Finch *Ortygospiza atricollis*. Bull. Brit. Orn. Club, **83**, pp. 141–146.

WHITE, C. M. N.
1962a. A check list of the Ethiopian Muscicapidae (Sylviinae), Parts II and III. Occ. Pap. Nat. Mus. So. Rhodesia, **26B**, pp. 653–738.
1962b. A revised check list of African Shrikes, Orioles, Drongos, Starlings, Crows, Waxwings, Cuckoo-shrikes, Bulbuls, Accentors, Thrushes and Babblers. iv+176 pp. Lusaka.
1963. A revised check list of African Flycatchers, Tits, Tree Creepers, Sunbirds, White-eyes, Honey Eaters, Buntings, Finches, Weavers and Waxbills. vi+218 pp. Lusaka.

WOLFF-METTERNICH, F.
1956. Biologische Notizen über Vögel von Fernando Po. Journ. f. Orn., **97**: pp. 274–290.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 | November 13, 1968 | No. 8

Geographical Variation in the Canary *Serinus sulphuratus*

Austin L. Rand

Chief Curator, Zoology, Field Museum of Natural History

This canary ranges widely east and south of the African equatorial forest with a favorite habitat of grasslands with many scattered trees and shrubs. It shuns the forest and also thick brush. Although widespread, it is often local in occurrence, and is absent from some of the more arid areas, such as much of western South Africa and eastern Kenya. In terms of political units the species range is from western Kenya, Uganda, and adjacent Congo south to Cape Province, and west across the continent through Northern Rhodesia (and parts of adjacent Congo) and Angola.

The main geographical variation is of the "more or less" type: in general size (wing length) and size of bill (not only in length, but even more so in depth and consequent bulk), and in coloration (yellowishness or greenishness of plumage). The extremes, the large, very heavy-billed, green bird from Cape Province, and the smaller, moderate-billed, and yellower bird from Uganda, etc., appear sharply different.

But there are intermediates of various sorts. Size and color do not always march together, and neither follow uniformly smooth clines, although some could be considered stepped reversing clines. To sketch this briefly:

The larger-billed, green-yellow Cape Province bird is replaced by a moderately yellow, moderately large-billed bird in northeastern South Africa; a small-billed, yellow bird occurs from Southern Rhodesia to Uganda, a small-billed, moderately green bird in Angola, and a moderately large-billed, moderately green-yellow bird in Kenya.

The difficulty of codifying this variation in terms of species and subspecies is shown by various taxonomic treatment. Roberts (1948

Library of Congress Catalog Card Number: 68-59024

(6th impression), Birds of South Africa, pp. 367–368) recognized two species: *S. sulphurata* with three subspecies, and *S. shelleyi* with none. The revised 1957 edition recognizes only one species with three subspecies, as does White (1963, Revised Check-list Afr.—finches—, p. 771) (but not all the same three that Sclater, 1930, Syst. Av. Aethiop., p. 816, recognized), while Clancey (1966, Durban Mus. Novit., **7**, pt. 13, p. 608) recognizes five races. Thanks to the series in Field Museum of Natural History, and the loan of material from the Museum of Comparative Zoology (courtesy of Dr. R. A. Paynter), the American Museum of Natural History (courtesy of Dr. Dean Amadon), and the United States National Museum (courtesy of Dr. G. E. Watson), it is possible to re-evaluate the situation with results differing somewhat from all the above. Perhaps the most notable of the changes is the recognition of the remarkable similarity between the populations from Kenya and those of the far distant southern Portuguese East Africa–Natal area. Angola birds are similar to these in color but not in bill size.

The problem can be considered from one point of view as lumping or splitting and the identification of specimens. But, from another point of view, the subspecies concept is more meaningful when considered as a way of codifying geographical variation with names so we can more easily talk about it. How many names are useful for this? Two treatments are possible: one, using two, or the other, using five subspecies names.

I. From a broad, over-all point of view, only two names could be used:

1. *S. s. sulphuratus* Linnaeus, 1776

   Range.—Cape Province.

   Diagnosis.—The largest, most heavy-billed, and greenest birds, with a dark olive breast band contrasting with the vivid yellow throat.

   Remarks.—This is the only population that is clearly separate from all the others.

2. *S. s. sharpei* Neumann, 1900

   Range.—That of the species north of Cape Province.

   Diagnosis.—This includes variable populations, but in color and size all are separate from the above in being less greenish and more yellowish; most populations are also smaller in size.

II. If this treatment be not accepted, it becomes necessary to use at least the five subspecies outlined below:

1. *S. s. sulphuratus* Linnaeus, 1776—Cape of Good Hope

   Range.—Cape Province.

   Diagnosis.—The darkest, greenest subspecies, with distinct dark olive breast band, also larger and more heavy-billed.

2. *S. s. wilsoni* Roberts, 1936—Kloof, Natal

   Synonym: *S. s. languens* Clancey, 1962, Durban Mus. Novit., 6, pt. 15, p. 193—Sul do Save, southern Portuguese East Africa.

   Range.—From Natal and Orange Free State to southern Portuguese East Africa.

   Diagnosis.—Like *sulphuratus,* but yellower on breast, flanks, and upper parts.

   Remarks.—*S. s. languens* was described as like *wilsoni* in color but smaller. Male wing 74–78 (av. 76) vs. 80.5–85.5 (av. 83.1), but see measurements in table. At most, this can be considered a slight tendency toward the smaller, brighter yellow *S. s. shelleyi* to the north.

3. *S. s. shelleyi* Neumann, 1903—Kafuro, northeastern Tanganyika.

   Synonym: *S. s. loveridgei* van Someren, 1921.—Lumbo, Portuguese East Africa.

   Range.—Southern Rhodesia, extreme southern Nyasaland, and northern Portuguese East Africa, presumably across central Tanganyika to Uganda and adjacent Congo.

   Diagnosis.—Differs from both the above in being yellower, the olive breast band being faint or obsolete, in the shorter wing, and in the much smaller bill, more evident in its lesser bulk than its somewhat shorter length.

   Remarks.—A female from Lumbo, northern Portuguese East Africa (the type locality of *loveridgei*) is small, wing 72, culmen 10, and very yellow, agreeing with females of *shelleyi* from Uganda in this). Vincent (1936, Ibis, p. 116) says that *shelleyi* from the littoral of Portuguese East Africa are smaller than those from inland.

   Four specimens from eastern southern Nyasaland area, and two from Southern Rhodesia are slightly greener than Uganda *shelleyi* but are best placed here.

4. *S. s. frommi* Kothe, 1911—Namanjera southwestern Tanganyika.

Range.—Southwestern Tanganyika, Northern Rhodesia (and probably adjacent Congo and northern Nyasaland) and Angola.

Diagnosis.—A small subspecies like *shelleyi* with a small bill but greener, with a more pronounced olive breast band, thus approaching in color both *wilsoni* and *sharpei.*

Remarks.—This name has usually been placed in the synonymy of *shelleyi,* although the characters of this race, greenishness and small bill, have been pointed out by Traylor (1962, Publ. Cult. Co. Diam. Ang., Lisboa, no. 58, p. 130).

I have not seen the type of *frommi* which is from Namanjera, in Ufipa, latitude 7° 34′ S., longitude 31° 07′ E., but the description says ". . . like *sharpei* but smaller—and in regard to color—under parts sulphur yellow with breast and flanks greenish yellow. . . ." I have a single specimen from Tukuyu, latitude 9° 16′ S., longitude 33° 38′ E., that agrees well with this, and with two Northern Rhodesia birds (Ndola and Lundazi) and most Angola birds.

From northern Nyasaland (Vipya Plateau, 6,000 ft.) I have but a single female (= ♂?) wing 76, culmen 12 mm. It is much greener below than Uganda *shelleyi* and agrees with male *frommi.*

Certain specimens in Field Museum from Mt. Moco and Mt. Soque in Angola are much darker and greener than a series in the American Museum from various parts of Angola and one from Mt. Moco. The meaning of this discrepancy is not clear.

5. *S. s. sharpei* Neumann, 1903—Marangu, Kilimanjaro

Range.—Western Kenya highlands and Kilimanjaro.

Diagnosis.—Differs from its geographical closest relative *shelleyi* in being larger, larger-billed, and more greenish with a light olive breast band; very similar to the far distant *wilsoni.*

Remarks.—The main character of this subspecies, on the northwestern edge of the range of the species and separated from *wilsoni* by *shelleyi,* is one of geography. As

TABLE OF MEASUREMENTS

I found it difficult to measure the bill satisfactorily. The measurements used here are the result of remeasuring the whole series in one day. Larger bills tend to be very much more massive than shorter ones, so that the observable differences are greater than measurements indicate.

	Wing (mm.)	Culmen (mm.)
S. s. sulphurata		
Cape Province sex ?	(9) 81–87 (av. 83.6)	(9) 12–14 (av. 13)
S. s. wilsoni		
Southern Portuguese East Africa ♂	(4) 77–79 (av. 78.1)	(4) 12–13 (av. 12.7)
Natal sex ?	(6) 81–87 (av. 83.6)	(6) 12–13.5 (av. 12.7)
S. s. shelleyi		
Uganda ♂	(10) 76–78 (av. 76.8)	(10) 11–12 (av. 11.4)
Lake Kivu to Lake Tanganyika area ♂	(7) 76–80 (av. 77.2)	(7) 11–12 (av. 11.5)
Extreme southern Nyasaland ♂ ?	(4) 72–73 (av. 72.3)	(4) 10.5–11 (av. 10.7)
Southern Rhodesia ♂	(2) 76, 76	(2) 12, 12
S. s. frommi		
Angola ♂	(7) 77–80 (av. 78.5)	(6) 10.5–12 (av. 11.1)
Northern Rhodesia ♂	(2) 78–81	(2) 12, 12
S. W. Tanganyika ♂	(1) 80	(1) 11
S. s. sharpei		
Kenya ♂	(7) 77–84 (av. 81.5)	(7) 12–14 (av. 12.8)

wilsoni itself shows internal geographical variations, I hesitate to attempt to set forth small differences observable in the specimens in hand.

The recognizing of *sharpei* on the basis of geography alone may be questioned as it is the beginning of a checkerboard pattern of characters well known from elsewhere, as, for example, in the case of the parrot *Tanygnathus lucionensis* of the Philippines (Rand and Rabor, 1960, Fieldiana: Zoology, **35,** p. 420). However, as *sharpei* is the single instance of the reduplication of characters in the species *S. sulphuratus,* the above treatment is maintained.

GENERAL

In the above, the geographical variation of *Serinus sulphuratus* is outlined in general terms, and is also codified into subspecies frame-

work at two levels. The first, recognizing only two subspecies, would satisfy few workers. Transferring *wilsoni* of Natal, etc., to the subspecies *sharpei* would be especially unsatisfactory to many. Recognizing five subspecies is the only logical refinement, and would bring the treatment of this species more in line with the recent revisionary work on other species in South Africa. Even so, additional variation within subspecies: *frommi, shelleyi,* and *wilsoni* is indicated. An attempt to correlate variation with climatic and geographical factors was nt fruitful.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 NOVEMBER 14, 1968 No. 9

Intra-Relations of African Canaries, Genus *Serinus*

AUSTIN L. RAND

CHIEF CURATOR, ZOOLOGY, FIELD MUSEUM OF NATURAL HISTORY

In preparing the section of African canaries for a forthcoming volume of *Peter's Check-List of Birds of the World,* I found a welcome guide in White's 1963 *Revised Check-List of African Flycatchers. . . Finches . . . and Waxbills.* However, I have made some changes in the arrangement of the species, and a few in species and subspecies limits.

Before going on to detail, the list of 25 species is presented with, where appropriate, the more aberrant subspecies included. Some of the latter have been considered, and perhaps will prove to be separate allopatric species. The 25 species recognized are arranged into six groups to indicate relationships and to aid discussion.

AFRICAN *SERINUS*

GROUP I

1. *canicollis* (including *flavivertex*)
2. *nigriceps*

GROUP II

3. *citrinelloides*
4. *frontalis*
5. *capistratus*
6. *koliensis*
7. *scotops*

GROUP III

8. *leucopygius*
9. *atrogularis* (includes *reichenowi, xanthopygius,* and *rothschildi*; *flavigula* is considered a mutant)

Library of Congress Catalog Card Number: 68-59025

No. 1060

10. *citrinipectus* (of hybrid *atrogularis* × *mozambicus* origin)
11. *mozambicus*
12. *donaldsoni*
13. *flaviventris* (includes *maculicollis* and *dorsostriatus*)
14. *sulphuratus*
15. *albogularis*

GROUP IV

16. *gularis* (includes *reichardi*)
17. *mennelli*
18. *tristriatus*
19. *menachensis*

GROUP V

20. *striolatus* (includes *whytii*)
21. *burtoni* (includes *melanochrous*)
22. *rufobrunneus*
23. *leucopterus*

GROUP VI

24. *totta* (includes *symonsi*)
25. *alario* (includes *leucolaema*)

This list is not the only arrangement possible, but is a compromise. Notably, Group II might have been placed first, Group V might have preceded Group IV. But, this is an attempt to put first the forms most like the Eurasian *Chloris–Serinus–Carduelis–Spinus* group, from which the African forms presumably originated, and place last, the most different African species without obvious close relatives elsewhere.

In making this arrangement, like White, I found it impractical to use the four genera in which Sclater (1930, *Systema Avium Aethiopicarum*) grouped them:

1. *Spinus* for the birds with wedge-shaped, fine-pointed bills (vs. stubby or heavy bills with curved culmen):
   nigriceps, frontalis, citrinelloides and *totta*.

b. *Serinus* for the predominantly yellow-green species:
   mozambicus, sulphuratus, etc.

c. *Poliospiza* for the predominantly grey-brown species:
   tristriatus, atrogularis, gularis, burtoni, albogularis, etc.

d. *Alario* for the one black, chestnut and white species:
   alario.

The other proposed genera, including the eight genera or subgenera proposed since 1920, are not recognized.

Certain lines of evident species relationship cut across that indicated by the unit characters used by Sclater. General similarities in plumage and pattern seemed the most useful in arranging the species. In regard to distribution, it must be remembered that almost all are non-forest birds in Africa, and thus range patterns exclude for the most part the tropical rain forests of the Congo and West Africa.

The six groups and their species are discussed below. The generalized range is given for each species.

Group I

1. *canicollis*—Eastern Africa: Eritrea to Cape Province; west to Angola.
2. *nigriceps*—Northeast Africa: (Ethiopia) above 8,000 feet.

Both are predominantly yellow-green species with rump only slightly yellower than back; *canicollis* (including *flavivertex*) is a rather plain species with a stubby bill; head pattern restricted to a dark area through eye and a yellowish forecrown; the female is duller, plain below; but the immature is more brownish above, whitish below and quite heavily streaked, both above and below. It appears to be distantly related to *S. canarius* and *S. serinus*. The conspicuous geographical variation includes: grey on back and sides of neck in the South African *S. c. canicollis*, lacking in other races; and tail being yellow or black: six subspecies.

S. nigriceps is also a green-yellow bird, but with a black "hood" (i.e., head and neck) in the male. It has a rather more slender bill than *caniceps* and slightly larger tarsus and toes and has been put in *Spinus*. No subspecies. While those two species are not particularly closely related, they seem as close to the Eurasian members of *Serinus-Spinus* group as to any of the African members, and thus are placed first.

Group II

3. *citrinelloides*—Eastern Africa: Eritrea to Kenya, eastern Northern Rhodesia and northern Portuguese East Africa (3 subspecies).
4. *frontalis*—Eastern Africa: Uganda and adjacent Congo, to northeastern Northern Rhodesia (? and subspecies Angola?)
5. *capistratus*—Gabun to Angola and south and east of the forests to north end of Lake Tanganyika.

6. *koliensis*—East Africa: eastern Congo to western Kenya.
7. *scotops*—South Africa.

These five species of small, yellow-green birds with rump a little yellower than the back, form a closely intra-related group despite the differences in bill shape and in sexual dimorphism. The bill is thinnest and most pointed in *frontalis,* and becomes progressively more stubby and heavier through *citrinelloides, capistratus, koliensis,* and *scotops.* Sexual dimorphism in color is pronounced in *frontalis, capistratus,* and some populations of *citrinelloides,* in all of which the males have a black mask (lacking in all females) and, correlated with this, are unstreaked below. The females of *citrinelloides* and *capistratus* are heavily streaked below, while that of *frontalis* is plain yellow. Sexual dimorphism in color is much less in *koliensis, scotops,* and some populations of *citrinelloides,* in which the black mask is reduced to dusky or greyish, or is absent, and both males and females are heavily streaked below.

Needless to say, the arrangement of these species has been various, *citrinelloides* and *frontalis* have been put in *Spinus* at times in the past, the others in *Serinus.* In recent treatments of the central African forms, *citrinelloides* and *frontalis* have been considered conspecific as have *capistratus* and *koliensis,* while Chapin (1954, Bull. Amer. Mus. Nat. Hist., **75*B***, pp. 606, 608) says that in eastern Congo where both *frontalis* and *capistratus* occur, but not together, their behavior is similar and if it were not for the differences in bill shape, he would consider them conspecific.

It is perhaps significant that the two most different central African forms, *frontalis* and *koliensis,* are the only ones with wide overlaps in ranges. What is found out about the manner in which *citrinelloides* meets *frontalis* and *koliensis* in western Kenya and eastern Uganda will probably influence our species concepts here. In the meantime, it seems advisable to keep them as species.

As in Group I, the relationship of this group to the *Serinus–Spinus* group of Eurasia seems evident, but cannot be pin-pointed.

Group III

8. *leucopygius*—northern Ethiopian region: Senegal to Eritrea.
9. *atrogularis*—Arabia, eastern and southern Africa: Eritrea to Cape Province and Angola.
10. *citrinipectus*—southern Portuguese East Africa area.
11. *mozambicus*—widespread outside forests in Ethiopian regions.

12. *donaldsoni*—northeastern and eastern Africa (Somalia to Tanganyika).
13. *flaviventris*—northeastern (Somalia), eastern and southern Africa and Angola.
14. *sulphuratus*—eastern Africa (Kenya) to South Africa (where chiefly eastern) and Angola.
15. *albogularis*—southern Africa, chiefly western.

In this group, the bill is of the stubby '*Serinus*' type, becoming very heavy in some species. Four species are predominantly yellow-green, while the remaining four others are predominantly grey-brown. The rump is differently colored, contrasting with the rest of the back, white in one species, yellow in the others; the "typical *Serinus*" head pattern (yellow or white forehead, and line over eye, a yellow or white fleck in cheek, a dark band through or back of the eye, and dark malar stripe) appears for the first time in this series and is usual, though is not invariably present even within a species (e.g., *atrogularis*).

These eight species form a fairly satisfactory group with stepped similarities, beginning with brown and grey, streaked species to various intermediate forms, to a species which is green-yellow in both sexes, and ending with a predominantly grey species.

S. leucopygius is a small grey-brown, streaked species with a white rump, completely lacking yellow or green. In part at least this is a geographical representative of the next species. *S. atrogularis*, also a small, grey-brown streaked species, has a yellow rump; the geographical variation in this species is great, and although the black-throated, eastern African form *somereni* is linked by intermediates to the very different white-throated, streaked *deserti* of South West Africa, the three northeastern forms, *reichenowi*, *xanthopygius*, and *rothschildi*, could, on present knowledge, be considered allopatric species. The close relationship of this species to the following yellow-green forms is also indicated by occasional occurrence of yellow-throated mutants in the northeastern forms of Africa, which White considered a separate species, *flavigula* (Rand, 1968, Bull. Brit. Ornith. Club, **88**, p. 116), and by the fact that *citrinipectus* of southern Portuguese East Africa is a species that seems to be of hybrid *atrogularis-mozambicus* origin (Irwin, 1961, Durban Mus. Novit., **6**, pt. 11, pp. 138–39).

S. mozambicus is small, greenish above, yellow below, with a "*Serinus* head pattern" of black and yellow, and with little sexual

dimorphism in color, though the female is duller. Even the young are similar but duller and with only a little spotting on breast.

The next species, *S. donaldsoni,* though much larger, and with a heavier bill, has a male that is somewhat of the yellow-green *S. mozambicus* type of coloration, with the head pattern more subdued, while the female is somewhat of the white-throated, streaked breast, brown-grey and whitish *S. atrogularis reichenowi* type!

S. flaviventris has a moderate bill and the male with the type of plumage that is similar to that of *donaldsoni* but more like that of *sulphuratus.* However, in the northern part of the range, the male has lower breast and abdomen white. The female has the upper parts brownish to olive green, streaked, and the under parts yellow and white, with breast more or less streaked. *S. flaviventris* as used here includes *dorsostriatus.*

S. flaviventris of South Africa, with six races, and *S. dorsostriatus* of East Africa, with two races, have usually been kept as separate species, with a wide geographical gap between their ranges. However, the differences between the two races that most closely approach each other is less than those characterizing some geographically isolated subspecies in such species as *atrogularis, striolatus, burtoni,* and *totta.*

The characters of the relevant races are:

S. f. damarensis; southern Angola and South West Africa to extreme northwestern Southern Rhodesia. (For revision of South African forms see White, 1967, Bull. Brit. Ornith. Club, **87,** p. 111 and references therein.) Male, wing (3) 70–75 (av. 71.1); tail (3) 53–55 (av. 54); culmen 9–10 mm.

S. f. dorsostriatus; northwest Tanganyika, southwestern Kenya, and central eastern Uganda: male like *damarensis* but upper parts greener with black streaking heavier, yellow of forehead wider; abdomen with a small patch of white, often obscured by surrounding yellow feathers; bill averages shorter. Male, wing (7) 72–77 (av. 73.4); tail (7) 47–52 (av. 50.7); culmen 8–10 mm. Female like that of *damarensis* in having conspicuous white abdomen and yellow breast more or less streaked, and differs chiefly in duller more olive upper parts with broader blackish streakings.

S. f. maculicollis; Somaliland to eastern Kenya and west to southeastern Sudan and northeastern Uganda. Male like that of *dorsostriatus* but yellow band on forehead much narrower, and whole abdomen conspicuously white; wing (9) 67–74 (av. 69.7); tail (9) 47–51 (av. 48.6); culmen 8–10 mm. Female: much like that of *dorso-*

striatus but white of abdomen more extensive, extending onto lower breast; streaking on breast more restricted sometimes forming a necklace across the yellow lower throat-upper breast.

The most extreme of the yellow-green series is *S. sulphuratus*, an intensely colored species with both male and female green and lightly streaked above, green-yellow below, unstreaked, and with the "typical *Serinus*" head pattern present but rather obscure, and even the immature are yellow-green, unstreaked below. The subspecies to be recognized have been discussed separately (Rand, 1968, Fieldiana: Zool., **51**, no. 8).

The change to the predominantly grey and white *S. albogularis* seems a sudden one, but in reality is not so great. *S. albogularis* looks in size, bill, and color much like *S. sulphuratus* that has lost all the yellow-green pigmentation except that on the rump and upper tail coverts.

Group IV

16. *gularis*—north Ethiopian region, northeastern and eastern Africa south to South Africa and Angola.
17. *mennelli*—Angola to Portuguese East Africa.
18. *tristriatus*—northeastern Africa: Eritrea to Ethiopia.
19. *menachensis*—southwestern Arabia.

In this group of brown-grey birds (without yellow or green), the rump is like the back in color; the side of the head is uniformly brown or blackish, except for a white eyebrow stripe in three species, and a black malar stripe in one, *tristriatus*. The crown tends to be more heavily streaked than the back due to the paler edges of the feathers which in several species are white and so extensive in the forecrown as to suggest an incipient white forehead. The throat tends to be white, and streaking of the breast and flanks none, to obscure or moderate. The bill is more or less stubby *Serinus* type but with a tendency for slight elongation and slight slenderness.

This group seems a fairly close-knit one. Perhaps the closest relative of the first species, *gularis*, is with *albogularis* to which it has a vague similarity; at the other extreme, *menachensis* seems to have no other relatives outside this group.

S. gularis has a white throat, brownish face, white eyebrow stripe, much white in forecrown, and in some subspecies there is moderate streaking on breast, flanks and back. Geographical variation is considerable, and the question of the specific status of *reichardi*, the

browner, more streaked bird of parts of eastern Africa, has been raised. Very close to *gularis* is *mennelli,* which co-exists with *gularis* and differs only in detail of coloration (black vs. brown face, etc.). *S. tristriatus* is a very plain bird with little streaking even on crown. The small area of white on chin and upper throat is bordered by black malar stripe, and the white eye stripe is narrow, but sharply defined. The Arabian representative, *menachensis,* is still plainer, but more streaked above and below.

Group V

20. *striolatus*—eastern Africa (Eritrea to Nyasaland).
21. *burtoni*—mountains of central Africa, Mt. Cameroon, Mt. Kenya, etc.
22. *rufobrunneus*—islands in Gulf of Guinea.
23. *leucopterus*—mountains of southwestern Cape Province.

This is a group of medium size to large, predominantly brown and grey canaries with moderate to heavy bills. Three species (in part at least) of the four have some tinge of greenish-yellow. The rump is colored like the back. The typical canary head pattern is present in one species (in brown and whitish), and suggested in another. Although not as closely knit a group as the three preceding ones, the limitations of a lineal arrangement justify grouping them here.

The only species with a widespread range is *striolatus,* which is heavily streaked above and on breast and flanks, and a pronounced "canary head pattern." It recalls a giant *S. atrogularis reichenowi* of eastern Africa, but it has greenish edgings to the wing quills, and one subspecies of restricted range, *S. s. whytii,* has yellow in throat and head, indicating the relationships with the yellow-green series. This last could be considered a separate species of restricted range in the highlands of southern Tanganyika and northern Nyasaland.

The relationship of the above species to the next, *burtoni,* of restricted, fragmented range, is indicated by the race *S. b. melanochrous* of the highlands of southern Tanganyika, which on the upper parts and head is much like *burtoni* but on the under parts has the streaking of *striolatus* and could be kept as a separate species. Another unusual, though minor character, of *melanochrous* is that the white in the forehead is due to white feather edging, as in *gularis,* not more solid areas as in *burtoni. S. burtoni* is a large canary, heavy billed, upper parts nearly uniform brown, with whitish tips to wing coverts (some races); a variable amount of white markings in forehead and

sides of head, and black and white in chin, suggesting a canary head pattern that is nearly lost, as the green of the plumage also has nearly disappeared, being present only as edgings to wing quills. Except for the one distinctly streaked subspecies mentioned above, the breast, belly, and flanks are ochraceous brown, with a little obscure streaking.

The Gulf of Guinea islands endemic *S. rufobrunneus* is a very plain reddish brown, above and below, bird with obscure streakings or mottling, throat paler with some dark markings on chin, and greater and medium wing coverts with pale rufous tips. Presumably, this is the result of a later invasion by *burtoni*-stock, after an earlier one gave rise to the genus *Neospiza* of Saint Thomas Island.

The South African species of limited distribution, *S. leucopterus,* a large, heavy-billed canary, is a rather plain, grey-brown, obscurely-mottled bird with white throat and abdomen and with the greenish influence appearing as a greenish tinge over back and wings. It could also be considered a relative of *albogularis,* or, more probably perhaps, of *gularis.* However, I put it here, agreeing with Clancey (1963, Durban Mus. Novit., **6,** pt. 19, p. 262).

GROUP VI

24. *totta*—South Africa.
25. *alario*—South Africa.

These two small species are not closely related, but are grouped as being the most extreme of the genus, without obvious specific relationships elsewhere in the genus. *S. totta* has been put in the genus *Spinus* because of the wedge-shaped bill. Even Roberts (1922, Ann. Transvaal Museum, **8,** p. 261) in coining so many new subgeneric names did not change this one. The pattern of obscurely mottled rufous-brown mantle, yellow-green striped head (without canary type pattern), and plain yellow, or yellow and rufous under parts, and the white line on the inner web of the outer tail feathers, is without parallel in the genus, though the contrasting yellow-green rump, of one race but not the others, is *Serinus* in character. In one race the female differs from the male only in degree; in the other, it is mostly rufous brown above, paler brown below. Although two rather different subspecies are recognized, this is an arbitrary decision, and some would consider them as two species.

S. alario (including *leucolaema* as a subspecies) with a stubby bill has had a genus proposed for it, because of its coloration, but Roberts (1922, Ann. Transvaal Museum, **8,** p. 261) wrote that he thought it

not far removed from *S. atrogularis*. Nicolai (1959, Zool. Jahrbücher., Syst., pp. 317–361) on the basis of behavior and hybridization relates it to *S. serinus* and *canicollis*. However, the coloration of the male with black hood, rufous mantle, and white lower breast and abdomen, and the female being drab-grey-brown and pale chestnut, and the similar but duller young with streaked upper parts provide little in the way of clues to relationships.

SUMMARY

This paper does not include the non-African species of the *Carduelis–Serinus–Spinus* group from which the African forms presumably evolved. The arrangement, new here, is based on similarities in patterns and is presumably phyletic. One genus, instead of several which have sometimes been used in the past, has been used for the above 25 species. A comprehensive species concept has also been used. Of the 25 species concerned, eight contain units which could be, and often have been, considered as separate species. These are indicated on the list on page 125. Only one of these is newly arranged here, the merging of *S. dorsostriatus* in the species *S. flaviventris*. In only one case is a traditional species treated as representing two species, i.e., *Serinus frontalis* and *S. citrinelloides*. These represent a group meriting further study.

The question of subspecies to be recognized have been extensively reviewed in the voluminous literature of African birds, of which the major items will be cited in the forthcoming volume of "*Peters*." The subjective element in the number of subspecies to be recognized makes a definitive treatment impossible.

At times it seems that the South African species have a disproportionate number of subspecies. But it must be remembered that the landscape there is very complex, with diversified vegetation and climate. Numbers of local workers, with large series and familiar with the birds in life, have reviewed the races, not always, it must be admitted, with the same results. I have had to make decisions. In only one case, *S. sulphuratus*, have I resurrected a name for a long overlooked race.

FIELDIANA · ZOOLOGY

Published by
FIELD MUSEUM OF NATURAL HISTORY

Volume 51 NOVEMBER 30, 1968 No. 10

A New Species of *Crotaphopeltis* (Serpentes: Colubridae) from Barotseland, Zambia

DONALD G. BROADLEY
UMTALI MUSEUM, RHODESIA

In 1962 Richard Japp presented a collection of Barotseland reptiles and amphibians to Field Museum of Natural History. This includes five snakes from Kalabo which belong to the genus *Crotaphopeltis*. Four specimens (FMNH 133041, 134253–5) are the common and widespread species *C. hotamboeia* (Laurenti), but the fifth represents an undescribed form. As this snake may be endemic to the Barotse floodplain, it is named:

Crotaphopeltis barotseensis, new species. Figures 1 and 2.

Holotype.—Field Museum of Natural History No. 134249, an adult female collected at Kalabo, Barotseland, Zambia, 24 March 1962 by Mr. Richard G. Japp (field number 1216).

Diagnosis.—A form of *Crotaphopeltis* differing from other species in the genus by having the upper postocular separated from the supraocular by a forward prolongation of the parietal, which enters the orbit. Dorsal scale rows 17–17–13: both *hotamboeia* and *degeni* normally have 17–19–15 rows, although the former may have 21 rows anteriorly (*ruiziensis* Laurent, 1963), while *tornieri* normally has 17-17–15 rows (Loveridge, 1933). In *barotseensis* and *degeni* the dorsal scales are smooth, glossy and iridescent, but in *hotamboeia* and *tornieri* the posterior dorsals are feebly keeled. The head of *barotseensis* is narrower than in the other forms, with a high rostral and no expansion in the temporal region.

Description.—Head distinct from neck; snout rounded; eye with a vertical pupil; body sub-cylindrical; tail 13.6 per cent of total length.

Library of Congress Catalog Card Number: 68-59374

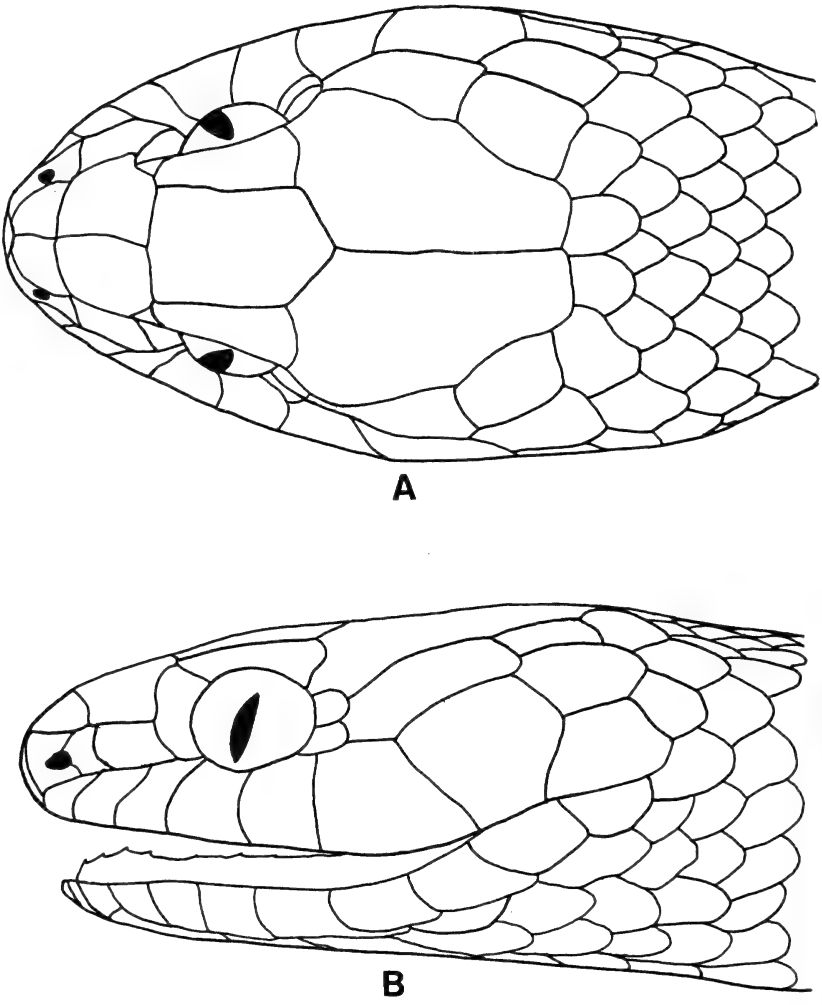


FIG. 1. Dorsal (A) and lateral (B) views of the head of holotype (FMNH 134249) of *Crotaphopeltis barotseensis*.

Rostral almost as deep as broad, barely visible from above; internasals two-thirds length of prefrontals; frontal straight-sided, 1.6 times as long as broad, longer than its distance from end of snout, two-thirds length of parietal; nasal divided, the posterior half excavate; loreal longer than deep; preocular 1, narrowly separated from frontal; postoculars 2, subequal in size, the upper separated from the supraocular by the parietal (fig. 1b); temporals 1+2; upper labials 8,

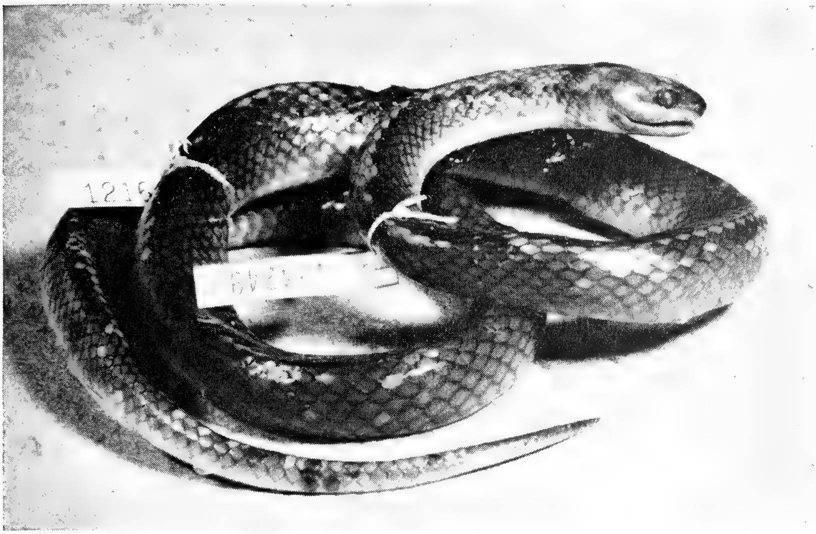


FIG. 2. Holotype (FMNH 134249) of *Crotaphopeltis barotseensis.*

the third, fourth and fifth entering the orbit; lower labials 10, the first five in contact with the anterior sublinguals, which are subequal to the posterior pair.

Dorsal scales quite smooth and iridescent with well-defined single apical pits, scale row reduction formula: $17 \frac{3+4\ (99)}{3+4\ (99)}\ 15 \frac{6+7\ (110)}{6+7\ (108)}\ 13.$

Ventrals 158, smooth; anal entire; subcaudals 38 pairs, smooth.

Maxillary dentition 15+II+1.

Coloration.—In alcohol: light grey-brown above, the scales dark-edged, gradually passing to paler brown below. No dark temporal patches.

Dimensions.—Head and body 470 mm., tail 74 mm. Head 20 mm. long, 12 mm. wide.

Habitat.—The upper Zambezi floodplain in Barotseland. This form may eventually be found on the Kafue Flats in Zambia, also in the Okavango–Chobe swamplands of northern Botswana.

Discussion.—It seems desirable to review the species included in the genus *Crotaphopeltis.* I agree with Gans and Laurent (1965) that the recognition of races of *C. hotamboeia* should be deferred until this wide-ranging species can be properly revised on a pan-African basis.

Crotaphopeltis degeni (Boulenger) has usually been recognized as a valid species (Pitman, 1938), but *C. tornieri* (Werner) was placed

TABLE 1.—Comparison of four species of *Crotaphopeltis*.

Character	*barotseensis*	*tornieri*	*degeni*	*hotamboeia*
dorsal scale rows	17 – 17 – 13	17 – 17 – 15	17 – 19 – 15	17 – 19 – 15 19 – 19 – 15 19 – 21 – 15 19 – 21 – 17 21 – 21 – 17
dorsal scales	smooth	feebly keeled posteriorly	smooth	feebly keeled posteriorly
ventrals	158	145 – 175	169 – 178	141 – 180
subcaudals	38	35 – 56	30 – 40	29 – 65
preoculars	1, not in contact with frontal	usually 2, rarely 1, often in contact with frontal	1, not in contact with frontal (rarely 2)	1, not in contact with frontal (rarely 2)
postoculars	2, subequal, upper not in contact with supraocular	2 (rarely 3), upper largest & in contact with supraocular	2, upper largest & in contact with supraocular	2 (rarely 1), upper largest & in contact with supraocular
Frontal length/breadth ratio	1.6	1.1 – 1.3	1.4 – 1.6	1.4 – 1.6
Maxillary dentition	15+II+1 (one maxilla)	16+II+1 (one maxilla)	17 to 18+II+0 (after Underwood	13 to 16+II+1 (various sources)
Habitat	floodplain	montane evergreen forest	floodplain	savanna
Temperament	?	inoffensive	fairly placid	irascible and vicious

as a subspecies of *C. hotamboeia* by Barbour and Loveridge (1928) and Bogert (1940) questioned its validity. I have re-examined the Rungwe Mountain series in the American Museum of Natural History and find that two specimens (AMNH 38986, 39203) are *tornieri,* the other four are *hotamboeia.* Sympatry at this locality establishes that *C. tornieri* is a good species. Table 1 compares the four species of *Crotaphopeltis* here recognized. I follow Laurent (1951) in including the arboreal species *duchesnii* (Boulenger), *werneri* (Boulenger) and *shrevei* (Loveridge) in the genus *Dipsadoboa.*

It would appear that an ancestral form had three postoculars (a variant in *C. tornieri,* and very rarely in *C. hotamboeia*). In *tornieri, degeni* and *hotamboeia* the upper two postoculars have fused, but in *barotseensis* the upper postocular has fused with the parietal, which consequently enters the orbit.

The smooth and shiny dorsal scales of *barotseensis* and *degeni* may indicate convergence rather than common ancestry. Both forms occupy semi-aquatic habitats.

Acknowledgements

I am grateful to the Field Museum of Natural History for allowing me to examine Japp's Barotseland collection and for publishing this paper. I also thank Dr. G. Underwood and Captain C. R. S. Pitman for unpublished data on *Crotaphopeltis degeni* material in the British Museum (Nat. Hist.), Dr. E. E. Williams (Museum of Comparative Zoology) and Dr. C. M. Bogert (American Museum of Natural History) for the loan of comparative material, and Mr. J. P. Coates Palgrave for photographing the holotype of *C. barotseensis*.

References

Barbour, C. M. and A. Loveridge

1928. A comparative study of the herpetological fauna of the Uluguru and Usambara Mountains, Tanganyika Territory, with descriptions of new species. Mus. Comp. Zool. Mem., **50**, pp. 87–265.

Bogert, C. M.

1940. Herpetological results of the Vernay Angola Expedition. Bull. Amer. Mus. Nat. Hist., **77**, pp. 1–107.

Gans, C. and R. F. Laurent

1965. Notes on a herpetological collection from the Somali Republic. IV. Snakes. Ann. Mus. Roy. Afr. Centrale (8) Sci. Zool., No. 134, pp. 47–70.

Laurent, R. F.

1951. Remarques à propos des Genres *Dipsadoboa* Günther et *Crotaphopeltis* Fitzinger. Rev. Zool. Bot. Afr., **44**, pp. 210–212.

1956. Contribution à l'herpetologie de la région des Grands Lacs de l'Afrique Centrale. I. Generalities. II. Chelonians. III. Ophidiens. Ann. Mus. Roy. Congo Belge (8), Zool., **48**, pp. 1–390.

Loveridge, A.

1933. Reports on the scientific results of an expedition to the Southwestern Highlands of Tanganyika Territory. VII. Herpetology. Bull. Mus. Comp. Zool., **74**, pp. 197–415.

Pitman, C. R. S.

1938. A guide to the snakes of Uganda. Uganda Soc. (Kampala).

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 SEPTEMBER 18, 1969 No. 11

The Larva of the Frog *Leptodactylus hylaedactylus* (Leptodactylidae)

W. RONALD HEYER
DIVISION OF AMPHIBIANS AND REPTILES
FIELD MUSEUM OF NATURAL HISTORY

AND

PHILIP A. SILVERSTONE
DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF SOUTHERN CALIFORNIA
AND LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY

No larva has been described for any member of the Marmoratus species group in the genus *Leptodactylus*. Recently Silverstone collected the larvae of *Leptodactylus hylaedactylus*, a member of the Marmoratus group. The purpose of this report is to describe these larvae, to discuss the habitat of the adults and larvae, and to comment on adaptations unique to this species within the genus.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

The report is based upon larvae from two foam nests from Regina, French Guiana, now on deposit at the Los Angeles County Museum of Natural History (tadpole lots LACM 42082, 5 individuals; 42083, 7 individuals). Methods for examining the preserved material follow Heyer (in press).

Priscilla H. Starrett (University of Southern California) and Robert F. Inger (Field Museum of Natural History) shared their knowledge of tadpole adaptation and morphology with us and read over the manuscript. Hymen Marx (FMNH) and Jay M. Savage (USC) critically reviewed the manuscript.

Arden H. Brame, Jr. and John W. Wright (LACM) facilitated the use of the reported specimens. Marion Pahl (FMNH) illustrated the larvae. Betty Peyton (FMNH) typed the final copy.

Silverstone was a National Defense Education Act Fellow at the University of Southern California during the field work and the completion of the report.

Library of Congress Catalog Card Number: 75-92691

We thank these individuals and institutions for their support.

Nomenclature

The Marmoratus group is poorly known, and requires a revision before populations can be associated with proper names. Some workers indicate that there is but one species (e.g., Rivero, 1961). Specimens collected by Silverstone from northeastern Brazil and French Guiana indicate that at least two species are involved. One species is small (snout-vent length 31 specimens, 13.7—20.5 mm., mean 17.1), has a blunt snout, and very large toe disks. The other species is larger (97 specimens, 15.7—24.9 mm., mean 20.6), has a more pointed snout, and small to moderately large toe disks. We follow Bokermann (1966) in regarding the type locality of *Adenomera marmorata* as probably around Rio de Janeiro, Brasil. Recent specimens from the probable type locality compare exactly with the small, blunt-snouted, large-disked specimens from French Guiana (*L. marmoratus*). All of the specimens collected at Regina, French Guiana, (LACM 44282–44378) are of the second species. The oldest name that could apply to this more slender-toed species is *L. hylaedactylus* Cope, 1868, with a type locality of the Napo or Upper Marañón Rivers, probably in Perú. We provisionally apply *L. hylaedactylus* to these specimens.

Diagnosis of Larva

Leptodactylus hylaedactylus is the only species within this genus known to lack both a spiracle and denticles in the tooth rows of the mouthparts.

Summary of Characteristics of Larva

Nostril midway between eye and tip of snout or nearer snout; distance between nares equal to interorbital distance; eye large, diameter 12–17% body length, mean 15; mouthparts subterminal; oral papillae in single row; oral disk entire; oral disk width 16–21% body length, mean 18; anterior oral papilla gap 73–92% oral disk width, mean 82; no denticles on tooth rows; beak weakly developed; no spiracle; dorsal fin origin at body-tail juncture, or origin on tail, posterior to body-tail juncture; tail height less than, equal to, or greater than body height; tail tip elongate and rounded to pointed; anal tube median; dorsum with uniform pattern, grey to brown in preservative; venter with suffusion of melanophores on throat region,

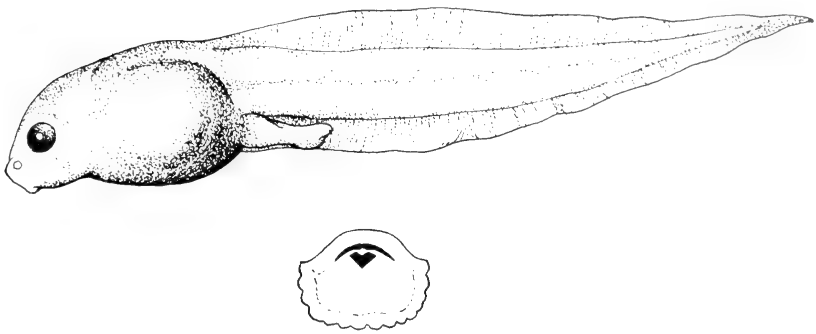


FIG. 1. Semi-diagrammatic representation of the larva of *Leptodactylus hylaedactylus*, stage 34. Upper figure: lateral view of larva, total length 12.5 mm. Lower figure: mouthparts, greatest width 0.8 mm.

few melanophores on belly, no melanophores on anal tube; no melanophores on tail fins, scattered melanophores on upper two-thirds of tail musculature; total length largest specimen, stage 34, 13.2 mm., stage 40, 12.6 mm.; body length 32–42% total length, mean 37 (fig. 1).

HABITAT

The town of Regina is located on the left bank of the lower Fleuve Approuague, one of the major rivers of French Guiana, at an altitude of 25 meters.

There is an airfield suitable for small planes immediately inland of the town. This unpaved field is partly bare ground and partly grass-covered, with the landing strip formed of metal plates laid upon the ground. The site was evidently formerly a marsh, and is bordered successively on the landward side by a ditch, a marsh, and a swamp. The field itself is dry land, but becomes quite muddy from rains.

The borders of the landing strip are marked by a series of metal and wooden markers. It was under one such marker that the tadpoles were found in two foam nests partially roofed over by soil. The nests were shallow circular cups, bearing a distinct raised rim. They were 35 mm. in diameter, and consisted of a thin layer of foam resting directly upon soil.

Large numbers of adult *L. hylaedactylus* were taken during the daylight hours beneath the runway markers. When the sheltering markers were lifted, these frogs attempted to escape into the surrounding grass. They shared their marker shelters with *Bufo marinus, Hyla rubra, Ameiva ameiva,* and *Mabuya mabouya.*

A much larger species, *Leptodactylus wagneri,* was taken in the neighbouring swamp calling at night, but *L. hylaedactylus* was not taken here; nor was *L. wagneri* taken on the airfield. *L. marmoratus,* the small, large-disked species mentioned above, was not taken on the airfield, but was found to be one of the most abundant anurans on the low, forested hills fringing the tributaries of the middle reaches of the Approuague. *L. hylaedactylus* and *L. wagneri* were not taken on these hills. All three species were distinct in their individual microhabitats.

The tadpole collection date was 25 July 1968, which is at the beginning of the principal French Guianan dry season.

Discussion

L. marmoratus complete metamorphosis in the foam nest in the incubating chamber. That is, the eggs hatch into larvae, but the larvae have enough yolk stores to carry them through to metamorphosis without feeding in the usual manner (Lutz, 1947). The available evidence indicates that this is also true of *L. hylaedactylus.* One of the foam nests contained five larvae at stage 40, with the forearms not quite protruding through the body wall. The yolk stores are noticeable even in these advanced-stage larvae. Eggs of members of the Marmoratus group are the largest within the genus *Leptodactylus.*

In forms which feed entirely upon yolk stores, such as *L. hylaedactylus* and *marmoratus,* natural selection apparently favors the reduction of mouthparts. *L. hylaedactylus* has no tooth row denticles, and the beak is not as well developed as in other *Leptodactylus* larvae examined.

The lack of a spiracle indicates that the larvae do not use gill respiration. This is consistent with the fact that the larvae are never in a truly aquatic environment. The forelimbs in the more advanced larvae are clearly underneath a sheet of skin indicating that an operculum has developed. It would be most interesting to have a series of very young larvae in order to determine whether a spiracle is ever formed while the operculum develops.

References

Bokermann, W. C. A.

1966. Lista anotada das localidades tipo de anfibios brasileiros. Serviço de Documentação, Cidade Universitaria, São Paulo. 181 pp.

HEYER, W. R.
In press. Studies on the genus *Leptodactylus* (Amphibia, Leptodactylidae). II. Diagnosis and distribution of the *Leptodactylus* of Costa Rica. Rev. de Biol. Trop.

LUTZ, B.
1947. Trends towards non-aquatic and direct development in frogs. Copeia, **1947** (4), pp. 242–252.

RIVERO, J. A.
1961. Salientia of Venezuela. Bull. Mus. Comp. Zool., Harvard, **126** (1), pp. 1–207.

FIELDIANA · ZOOLOGY

Published by
FIELD MUSEUM OF NATURAL HISTORY

Volume 51 | September 19, 1969 | No. 12

Veronicellid land slugs from the New Hebrides, with description of *Semperula solemi*, new species

Lothar Forcart
Naturhistorisches Museum, Basel[1]

Previous records of New Hebridean land slugs belonging to the family Veronicellidae were given by Collinge (1900), Grimpe and Hoffmann (1925) and Hoffmann (1929). Collinge (1900) reported three species from Vate Island (=Esafate). One of these, *Veronicella brunnea*, he described on the basis of a single specimen. Two specimens were referred to *Vaginula leydigi* (Simroth) and one to *V. hedleyi* (Simroth). Both specimens were described originally by Simroth (1889, p. 552) from material collected in Brisbane, Queensland. The original specimens could not be located in the British Museum (Natural History) by J. F. Peake and they are presumed lost. Although he had not seen these specimens, Hoffmann (1925, pp. 120, 190, 191), synonymized *Vaginula leydigi* of Collinge with *Laevicaulis alte* (Férussac) and placed both *Veronicella brunnea* and *Vaginula hedleyi* in the synonymy of *Vaginulus* (*Sarasinula*) *plebeius* Fischer. On the basis of Collinge's descriptions and illustrations, I concur in this action.

Grimpe and Hoffmann (1925) reported on the anatomy of seven specimens belonging to *Vaginulus plebeius* from Malo Island. They could not be located in the Naturhistorisches Museum, Basel collection. Hoffmann (1929, pp. 115–117) recorded two examples of *V. plebeius* from Espiritu Santo. These are preserved in the British Museum (Natural History).

This paper reports on material collected by Borys Malkin in 1958 and several sets collected by British zoologists in the 1920's and 1930's. For the loan of this material, I am indebted to Dr. Alan

[1] Present address: Zürcherstrasse 9, Basel, Switzerland.

Library of Congress Catalog Card Number: 71–92690

Solem, Field Museum of Natural History, Chicago, and to Mr. John Peake, British Museum (Natural History), London. The illustrations are by O. Garraux, Basel.

The following abbreviations indicate the depository of mentioned specimens:

BMNH—British Museum (Natural History), London
FMNH—Field Museum of Natural History, Chicago
NMB—Naturhistorisches Museum, Basel

SYSTEMATIC REVIEW

Previously recorded data was summarized by Solem (1959, pp. 41–42). He had no material available for study, so compiled the scattered records. Following the results of earlier studies, I recognize three genera in the available material, *Laevicaulis, Vaginulus* and *Semperula.*

Genus **Laevicaulis** Simroth, 1913

Laevicaulis Simroth, 1913, *in* Voeltzkow, Reise Ostafrika, 3 (3), pp. 147, 202. Type species: *Vaginula comorensis* Fischer, 1883 by subsequent designation of Pilsbry (1919, p. 316).

Eleutherocaulis Simroth, 1913, *op. cit.*, pp. 187, 202. Type species: *Vaginula comorensis* Fischer, 1883, by subsequent designation of H. B. Baker (1925, p. 15); Solem, 1959, Fieldiana: Zoology, **43**, p. 42.

Meisenheimeria Grimpe and Hoffmann, 1924, Zool. Anz., **58**, p. 177. Type species: *Vaginula frauenfeldi* Semper, 1885 by original designation.

H. B. Baker (1931, p. 137) mentioned "In an earlier paper (1925, Naut., **39**, p. 18), I followed Pilsbry's use of *Laevicaulis* in preference to *Eleutherocaulis,* but now realize that Simroth's own use (1913, p. 202) of the latter as the ranking term makes *Eleutherocaulis* the valid name and *Laevicaulis* the synonym." This opinion was accepted by Solem (1959, p. 42).

It contradicts Article 43 of the *International Code of Zoological Nomenclature,* which states that "The categories in the genus-group are of co-ordinate status in nomenclature. . . ." The selection of the name *Laevicaulis* by Pilsbry (1919, p. 316) as first reviser stands subsequently (Article 24 of the Code).

Laevicaulis alte (Férussac, 1821)

Vaginulus alte Férussac, 1821, Tabl. syst. Limaces, p. 14. Type locality: Pondicherry, India; Férussac, 1821, *in* Férussac and Deshayes, Hist. Nat. Moll. terr. fluv., pl. 8A, fig. 8 and pl. 8B, fig. 6 (1822).

Veronicella leydigi (Simroth), Collinge, 1900, *in* Willey, Zool. Res. Voy. N. Caledonia, **4**, p. 435.

Meisenheimeria alte f. *leydigi* (Simroth), Grimpe and Hoffmann, 1925, Nova Caledonia, Zool., **3** (3), p. 384.

Meisenheimeria alte (Férussac), Grimpe and Hoffmann, 1925, Zeits. wiss. Zool., **124** (1), pp. 26–31; Hoffmann, 1925, Jena. Zeits. Naturwiss., **61** (1/2), pp. 120–129, 226–228.

Laevicaulis alte (Férussac), Forcart, 1953, Ann. Mus. Roy. Congo Belge, Tervueren, Zool., **23**, pp. 63–68.

Eleutherocaulis alte (Férussac), Solem, 1959, Fieldiana: Zool., **43**, p. 42.

Range.—Vate and Espiritu Santo.

Material examined.—Vila, Vate (2 specimens, FMNH 160006 collected July 1958 by B. Malkin). Santo, Espiritu Santo (7 specimens, FMNH 160007 collected July 1958 by B. Malkin).

Genus **Vaginulus** Férussac, 1821

Vaginulus Férussac, 1821, Tabl. syst. Limaces, p. 13. Type species: *Vaginulus taunaisii* Férussac, 1821 by subsequent designation of Stoliczka (1873, Jour. Asiat. Soc. Bengal, **42**, p. 35).

Subgenus **Sarasinula** Grimpe and Hoffmann, 1924

Sarasinula Grimpe and Hoffmann, 1924, Zool. Anz., **58**, p. 177. Type species: *Vaginulus plebeius* Fischer, 1868 by original designation.

Considerable controversy has existed concerning the taxonomic position of *Sarasinula.* Originally described as a genus, it was synonymized with *Imerinia* Cockerell (1891, type species: *Vaginula grandidieri* Crosse and Fischer, 1871 by subsequent designation of Cockerell and Collinge, 1893, p. 195) by H. B. Baker (1925a, p. 17). While Hoffmann (1927, p. 3) accepted Baker's proposal, at a later time H. B. Baker (1931, pp. 135–136) separated the two taxa. He classified *Sarasinula* as a section of *Angustipes* Colosi, 1922, which he placed as a subgenus of *Vaginulus,* while *Imerinia* was considered generically distinct. H. B. Baker (1925b, 1931, p. 136) grouped the subsections of *Vaginulus* as follows:

- Genus *Vaginulus* Férussac, 1821
  - Subgenus *Vaginulus,* s. s.
    - Section *Vaginulus,* s. s.
    - Section *Phyllocaulis* Colosi, 1922
  - Subgenus *Angustipes* Colosi, 1922
    - Section *Angustipes,* s. s.
    - Section *Latipes* Colosi, 1922
    - Section *Sarasinula* Grimpe and Hoffmann, 1924

As a result of additional studies and the fact that the taxon "section" is not accepted for general use, I propose to divide *Vaginulus* into five subgenera—*Vaginulus,* s. s., *Phyllocaulis, Latipes, Angustipes,* and *Sarasinula.*

KEY TO THE SUBGENERA OF *VAGINULUS*

1. Hindgut and vagina enter body wall separated 2
   Hindgut and vagina enter body wall in close juxtaposition 3

2. Penis with spatha . . . . *Phyllocaulis*
   Penis without spatha . . . . *Vaginulus*, s. s.

3. Canalis junctor enters bursa of receptaculum seminis near apex . . . . . . *Latipes*
   Canalis junctor enters bursa of receptaculum seminis near base 4

4. Bursa of receptaculum seminis sessile . . . . *Angustipes*
   Receptaculum seminis with bursa and pediculus . . . . *Sarasinula*

Vaginulus (Sarasinula) plebeius Fischer, 1868

Vaginulus plebeius Fischer, 1868, Jour. de Conchy., **16**, p. 146. Type locality: New Caledonia.

Veronicella brunnea Collinge, 1900. *In* A. Willey, Zool. Res. Voy. New Caledonia, **4**, p. 435, pl. 41, figs. 18–23. Type locality: Vate, New Hebrides.

Veronicella hedleyi (Simroth), Collinge, 1900, loc. cit.

Sarasinula plebeja (*sic*) (Fischer), Grimpe and Hoffmann, 1925, Nova Caledonia, **3** (3), pp. 343, 353, 357–362, 365–366, 377–378, 383, text figs. 2a, 3a, 4a, 5a, 5c, 6a, 6c, 7, 8a, 9, pl. 6, figs. 1–3.

Imerinia plebeja (*sic*) (Fischer), Hoffmann, 1929, Zool. Anz., **84**, (5/6), pp. 108, 115–117.

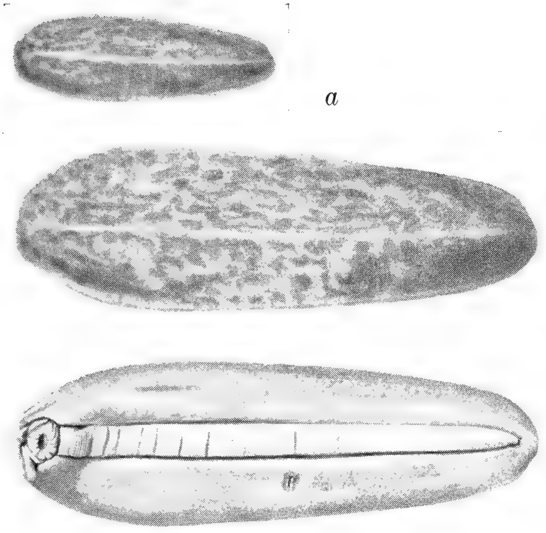
Angustipes (*Sarasinula*) *plebeius* (Fischer), Solem, 1959, Fieldiana: Zool., **43**, p. 41.

Range.—Vate, Omba, Malekula, Espiritu Santo, and Malo.

Material examined.—New Hebrides (4 specimens, BMNH 1936.9.52–55 collected by T. Harrison): Omba (=Aoba), Bankaharijitoa above Dunduy at 1,500–2,000 ft. elevation in forest under logs and bark (13 specimens, FMNH 160012 collected August 1958 by B. Malkin). Malekula (1 specimen, BMNH 1936.12.9.10): Ounua (1 specimen, BMNH 1936.12.9.25 collected April 1929 by L. E. Cheesman). Espiritu Santo, Hog Harbour (2 specimens, BMNH 1929.6.25.4–5 collected by J. R. Baker).

Genus **Semperula** Grimpe and Hoffmann, 1924

Semperula Grimpe and Hoffmann, 1924, Zool. Anz., **58**, p. 177. Type species: *Vaginula idae* Semper, 1885.



a

b

c

FIG. 1. *Semperula solemi*, new species. Paratype from Santo, Espiritu Santo. FMNH 160020. *a*, dorsal view, actual size; *b*, dorsal view, 2 ×; *c*, ventral view, 2 ×.

Semperula solemi, new species. Figures 1–3.

Diagnosis.—A species of the genus *Semperula* that is closely related to *S. wallacei* (Issel), but separable externally by the shorter distance of the female gonopore from the pedal groove and the narrower sole.

Description.—External features (fig. 1): Ground color of notum yellowish-brown with gray speckles. Hyponota and sole with same ground color, some specimens possessing fine dark spots on the hyponota. Notum with fine pores and very fine papillae. Sole width half or less than half width of one hyponotum. Female opening a transverse slit in hyponotum, usually surrounded by darker pigmentation, but the latter indistinct in some specimens. Internal anatomy typical of genus *Semperula*, with penis (figs. 2–3) having a longer and more slender glans than in *S. wallacei* (see Hoffmann, 1941, p. 230, fig. 1). Penial gland consists of a pointed papilla and about 16 glandular tubules that are partly forked and are compacted to form an "S"-shaped bundle (fig. 3, *b*).

Range.—Vate and Espiritu Santo.

Holotype.—Santo, Espiritu Santo, New Hebrides. Field Museum of Natural History 160022. Collected by Borys Malkin in July 1958.

FIG. 2. *Semperula solemi*, new species. Holotype. Penis drawn from a transparent preparation, 15×.

Paratypes.—Vate: Vila (22 specimens, NMB 11.007-b, FMNH 160016–7). Espiritu Santo: Santo (38 specimens, NMB 11.007-a, FMNH 160010, FMNH 160018–21 collected by B. Malkin in July 1958).

Remarks.—Measurements of the nine largest examples from each locality are given in Tables I and II. Definitions of the measurements are:

1. Notum
   - 1a. Notum length, bowed measurement
   - 1b. Notum width, bowed measurement
   - 1c. Length/width ratio
2. Right hyponotum
   - 2a. Width at midpoint
   - 2b. Width at female pore
3. Sole
   - 3a. Width at midpoint
   - 3b. Ratio of right hyponotum width (2a) to sole width (3a)
4. Female opening
   - 4a. Distance from anterior end of notum
   - 4b. Distance from posterior end of notum

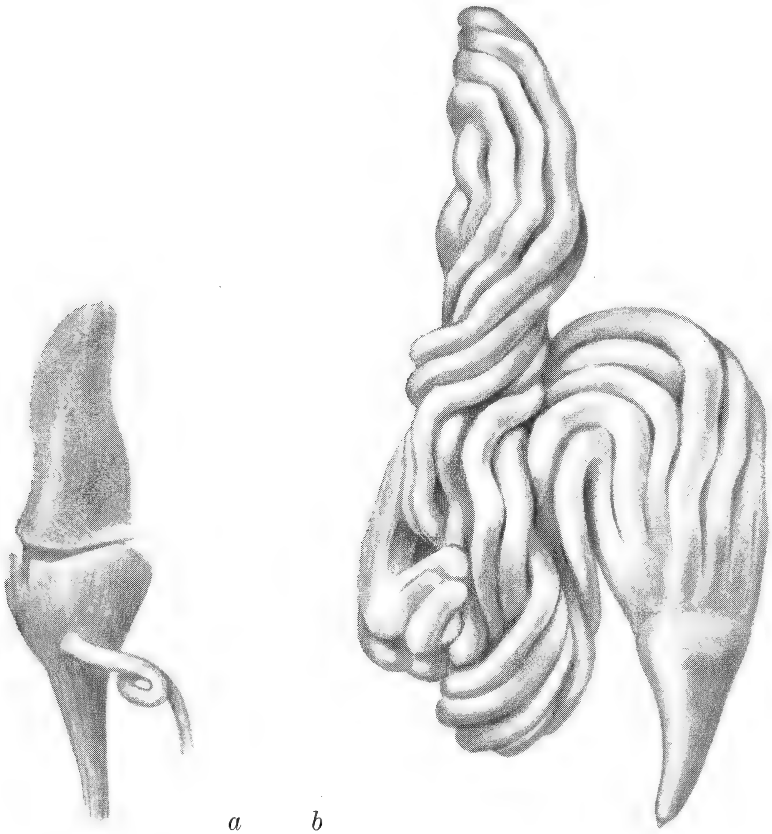


FIG. 3. *Semperula solemi*, new species. Paratype from Vila, Vate. *a*, penis 15×; *b*, penial gland, 15×.

4c. Distance from middle of pore to pedal groove
4d. Ratio of 4a/4b
4e. Ratio of 2b/4c

All measurements are in millimeters and were made to conform with those used by Hoffmann. There are no significant differences between the two samples. All specimens had been preserved in 70 per cent alcohol.

Dissection showed that the penis is longer, more slender, and has a finely-papillated glans (see figs. 2, 3) when compared with *Semperula wallacei* as described by Hoffmann (1941, p. 230), fig. 1).

TABLE I.—Measurements of *Semperula solemi*, new species, from Santo, Espiritu Santo.

Measured characters —	1a	1b	1c	2a	2b	3a	3b	4a	4b	4c	4d	4e
Holotype (dissected)	41.7	15.4	2.7	5.5	4.8	2.0	2.4	19.8	15.7	2.2	1.3	2.5
Paratypes (dissected)	41.3	15.5	2.7	5.2	5.3	1.8	2.9	18.7	19.5	2.1	1.0	2.5
	40.3	14.5	2.8	5.2	4.7	1.9	2.8	17.7	14.8	2.0	1.2	2.4
	40.0	12.2	3.3	4.5	4.2	1.9	2.4	16.3	17.0	1.6	1.0	2.6
(dissected)	37.5	15.0	2.5	5.3	4.7	2.7	2.0	19.1	15.1	2.0	1.3	2.4
	36.6	14.5	2.5	4.5	4.5	1.9	2.4	16.8	14.4	1.6	1.2	2.8
	36.3	14.4	2.5	5.2	5.2	2.3	2.3	17.8	16.2	2.3	1.1	2.3
	35.6	14.6	2.5	4.7	4.7	2.1	2.2	16.0	14.4	1.5	1.2	3.1
	34.7	14.3	2.4	4.5	4.5	1.9	2.4	14.0	15.9	1.6	0.9	2.8
Maximum value	41.7	15.5	3.3	5.5	5.3	2.7	2.9	19.8	19.5	2.3	1.3	3.1
Minimum value	34.7	12.2	2.4	4.5	4.2	1.8	2.0	14.0	14.4	1.5	0.9	2.3
Mean value	38.2	14.4	2.7	5.0	4.7	2.0	2.4	17.4	15.8	1.9	1.1	2.6

TABLE II.—Measurements of *Semperula solemi*, new species, from Vila, Vate.

Measured characters —	1a	1b	1c	2a	2b	3a	3b	4a	4b	4c	4d	4e
All are paratypes	44.4	19.0	2.3	5.3	5.3	2.1	2.5	18.6	15.7	2.0	1.2	2.6
(dissected)	39.0	13.7	2.8	3.8	3.2	2.1	1.8	17.5	17.1	1.4	1.0	2.3
	36.6	13.6	2.7	4.7	4.7	1.5	3.1	14.8	16.5	2.0	0.9	2.3
	35.8	11.3	3.7	4.3	4.3	1.8	2.4	16.3	16.2	1.5	1.0	2.9
	35.5	15.2	2.3	4.2	3.8	2.0	2.1	17.0	13.5	1.8	1.3	2.1
	33.4	13.8	2.4	4.4	4.4	1.5	2.9	13.6	13.5	1.7	1.0	2.6
(dissected)	33.4	16.2	2.1	4.4	4.6	2.0	2.3	14.3	16.7	2.4	0.9	1.9
	33.2	14.5	2.3	4.7	4.5	1.9	2.5	17.2	14.0	2.5	1.2	1.8
	30.5	13.3	2.3	4.2	4.2	1.4	3.0	15.3	15.7	2.2	1.0	1.9
Maximum value	44.4	19.0	3.7	5.3	5.3	2.1	3.1	18.6	17.1	2.5	1.3	2.9
Minimum value	30.5	11.3	2.1	3.8	3.2	1.4	1.8	13.6	13.5	1.4	0.9	1.8
Mean value	35.7	14.5	2.8	4.4	4.3	1.8	2.5	16.0	15.4	1.9	1.0	2.2

Semperula solemi is dedicated to Alan Solem, investigator of mollusks of the New Hebrides.

REFERENCES

Baker, H. Burrington

1925a. Nomenclature of Veronicellidae (*Vaginula*). Nautilus, **39** (1), pp. 13–18.

1925b. North American Veronicellidae. Proc. Acad. Nat. Sci., Philadelphia, **77**, pp. 157–184, pls. 3–6.

1931. Notes on West Indian Veronicellidae. Nautilus, **44** (4), pp. 131–137.

Cockerell, T. D. A. and W. E. Collinge

1893. A Check-list of the slugs. Conchologist, **2** (7), pp. 168–176 and (8), pp. 185–232.

Collinge, W. E.

1900. Report on the slugs. *In* A. Willey, Zoological Results of a Voyage to New Caledonia, New Guinea, Loyalty Islands, **4**, pp. 429–436, pls. 40–41.

Grimpe, G. and H. Hoffmann

1924. Diagnosen neuer Athoracophoriden. Zool. Anz., **58**, pp. 171–177.

1925. Die Nacktschnecken von Neu-Caledonien, den Loyalty-Inseln und den Neuen-Hebriden. *In* F. Sarasin and J. Roux, Nova Caledonia, **3** (3), pp. 339–476, pls. 5–6.

Hoffmann, H.

1925. Die Vaginuliden. Jena. Z. Natur., **61** (1/2), pp. 1–374, pls. 1–11.

1927. Ueber Vaginuliden aus den Reichsmuseum Stockholm. Ark. Zool., **19A** (25), pp. 1–39.

1929. Ueber einige Nacktschnecken von den Neuen Hebriden. Zool. Anz., **84** (5/6), pp. 108–118.

1941. Ueber einige Vaginuliden auf Grund bisher für verschollen gehaltener Typstücke. Zool. Anz., **136** (11/12), pp. 229–242.

Pilsbry, Henry A.

1919. A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum. Bull. Amer. Mus. Nat. Hist., **40**, pp. 1–370, 23 pls.

Simroth, H.

1889. Ueber einige *Vaginula*-Arten. Zool. Anz., **12**, pp. 551–556, 574–578.

1913. Ueber die von Herrn Prof. Voeltzkow auf Madagaskar und in Ostafrika erbeuteten Vaginuliden, nebst verwandtem Material von ganz Africa. *In* A. Voeltzkow, Reise in Ostafrica in den Jahren 1903–1905, **3** (3), pp. 129–216, pls. 13–17.

Solem, A.

1959. Systematics and zoogeography of the land and fresh-water Mollusca of the New Hebrides. Fieldiana: Zool., **43** (1), pp. 1–238, 34 pls., 8 figs.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 SEPTEMBER 30, 1969 No. 13

New Birds from Camiguin South, Philippines

AUSTIN L. RAND
CHIEF CURATOR, ZOOLOGY, FIELD MUSEUM OF NATURAL HISTORY

AND

DIOSCORO S. RABOR
ASSOCIATE, BIRDS, FIELD MUSEUM OF NATURAL HISTORY
RESEARCH PROFESSOR, BIOLOGY, MINDANAO STATE UNIVERSITY,
MARAWI CITY, PHILIPPINES

There is an island in the western Mindanao Sea called on the maps simply Camiguin, but we will call it Camiguin South to distinguish it from the island of the same name to the north of Luzon, which we will call Camiguin North as McGregor did in 1909. There has been confusion in the earlier literature.

In 1968 Rabor, as part of his continuing studies, stayed briefly on Camiguin South and made a collection there. Later, in making a preliminary study of the collection, he picked out several species for more study and sent them, along with his notes, to Rand to complete comparisons and descriptions. This paper is a report on four species. Further field work and a complete report on the birds of the island are contemplated.

Camiguin South, in the Mindanao Sea, lies about ten miles north of Mindanao and 50 miles southeast of Bohol. This volcanic island is about 9 by 13 miles in size, with a peak rising to over 5,000 feet. Although heavily populated, there are still forest areas.

Its ornithological history is short. The historic H.M.S. *Challenger* stopped here and sent a party ashore for a few hours on the afternoon of January 26, 1875. The following five species of common, widespread Philippine birds were collected, four of them from second growth and open country, and one a sandpiper: *Corvus macrorhynchus, Aplonis panayensis, Halcyon chloris, Nectarinia jugularis,* and *Actitis hypoleucos* (Tweeddale, 1877, Proc. Zool. Soc. London, p. 536).

Library of Congress Catalog Card Number: 79-99764

No. 1081

The next ornithological visitor was in 1921 when W. Cameron Forbes, Governor-General of the Philippines, "visited most of the islands of the group." He was accompanied at times by such luminaries as Leonard Wood, Worcester, McGregor, and Celestino. When the collections came to the Museum of Comparative Zoology Outram Bangs, 1922, Bull. Mus. Comp. Zool., **65**, pp. 77–84, reported on the more interesting specimens which included at least two species labeled from Camiguin [South]: *Lalage niger* and two specimens of *"Zosterops forbesi"=Z. everetti basilanica* collected on August 2, 1921. Until Rabor's 1968 work, no other bird work for this area has come to our attention. Rabor plans more work for 1968–69.

Four species are discussed in this paper: *Hypsipetes everetti, Hypothymus azurae, Dicaeum trigonostigma,* and *Zosterops nigrorum,* each with new subspecies—five in all.

Hypsipetes everetti

Delacour, *in* Delacour and Mayr, 1945, Zoologica, **30**, p. 112; Delacour, *in* Delacour and Mayr, 1946, Birds of the Philippines, p. 176; Rabor, 1955, Silliman Jour., **2**, p. 103; Rand and Rabor, 1959, Auk, **76**, pp. 102–104; Deignan, 1960, Peter's Check-list of Birds of the World, **9**, p. 288; deSchauensee and duPont, 1962, Proc. Acad. Nat. Sci. Phila., **114**, p. 163.

The treatment of the species limits of *everetti* and its naar relatives in the Mindanao area has changed several times in recent decades. This has resulted from the progressive increase in our knowledge of the ranges of the forms involved, an increase due to the progressive field work, especially that of Rabor, in Mindanao.

Basic was the discovery that *philippinus* did not range over all western Mindanao (Rabor, 1955, *contra* Delacour, 1946), and that both *everetti* and *philippinus* from the east, and *rufigularis* from the west, all met in the Lake Lanao area of western central Mindanao (Rabor, 1955; Rand and Rabor, 1959; deSchauensee and duPont, 1962).

Obviously, *rufigularis* cannot be conspecific with either *everetti* (*contra* Delacour, 1946) nor with *philippinus* (*contra* Rand and Rabor, 1959; Deignan, 1960).

Rabor, 1955, suggested that *rufigularis,* the only *Hypsipetes* of western Mindanao and Basilan was not monotypic but conspecific with *haynaldi* of the Sulu islands as the only *Hypsipetes* occurring there. This last is a form that is somewhat intermediate in appear-

ance between the yellow-olive *everetti* and the brown-tawny, white-bellied *rufigularis*, even if it is not intermediate geographically.

However, the discovery of another dark race of *everetti* on the isolated island of Camiguin South (where it is the only *Hypsipetes*), adds weight to keeping the dark *haynaldi* also in *everetti*, leaving *rufigularis* monotypic.

The following arrangement seems preferable:

H. philippinus; Luzon to eastern and central Mindanao; several races.

H. rufigularis; western central Mindanao west to Basilan; monotypic.

H. everetti; Samar to eastern and central Mindanao; also Sulu islands and Camiguin South; four races, see below.

Hypsipetes everetti samarensis Rand and Rabor

Range.—Samar and Leyte; probably Panaon birds are the same.

Diagnosis.—Upperparts predominantly olive green, crown little different but with lighter lanceolate tips to some feathers: throat buffy ochraceous (deep tawny) breast olive-tinged tawny; lower breast and abdomen yellow; flanks, yellowish olive.

Wing ♂ (10) 113–121 (av. 117 mm.); ♀ (10) 105–115 (av. 110.8 mm.); culmen ♂ (10) 28–31 (av. 29.9 mm.); ♀ (10) 27—28 (av. 27.7 mm.).

Hypsipetes everetti everetti Tweeddale

Range.—Dinagat and east and central Mindanao west to Lake Lanao area.

Diagnosis.—Like *samarensis* but upperparts brighter, clearer green (less golden or olive green); throat and upper breast brighter ochraceous; lower breast and abdomen being brighter, clearer yellow, and in flanks being less heavily washed with olive.

Wing ♂ (6) 118–125 (av. 122.3 mm.); ♀ (6) 112–118 (av. 114.8 mm.); culmen ♂ (6) 28–31 (av. 29.3); ♀ (6) 26–30 (av. 27.3 mm.).

Remarks.—There is considerable variation in Mindanao birds, and this results in an overlap with Samar and Leyte series.

Hypsipetes everetti haynaldi Blasius

Range.—Sulu Archipelago (Sulu and Tawi Tawi Islands).

Diagnosis.—Like *everetti* in having crown about like back, but differs in upperparts being considerably duller, darker, more brownish olive; in the throat and upper breast being darker and duller brownish without tawny tinge, and flanks deeper olive; also wing shorter (but not bill).

Wing ♂ (6) 107–116 (av. 110 mm.); ♀ (6) 107–112 (av. 109 mm.); culmen ♂ (6) 27–29 (av. 28 mm.); ♀ (6) 27–30 (av. 28 mm.).

Remarks.—This is a well-marked, but not a strikingly different race. I have to thank Dr. R. L. Zusi of the United States National Museum for the loan of the 12 Sulu Archipelago specimens. They were collected in September–November, 1891 by Worcester and Bourns.

Neither this form nor *everetti* is known from Basilan or western Mindanao where its place is taken by *H. rufigularis* of which it appears to be the ecological equivalent.

Hypsipetes everetti catarmanensis, new subspecies

Type.—Field Museum Natural History no. 284,445 from Camiguin South Island, Catarman Mt. between 2,000 and 4,000 feet. Adult male collected June 16, 1968 by D. S. Rabor.

Diagnosis.—Differs from the above three races in having the crown brownish black contrasting sharply with the rest of upperparts; differs in rest of upperparts being considerably darker greenish olive, in the darker brownish breast, in the darker olive flanks, and in larger size.

Wing ♂ (9) 126–136 (av. 129 mm.); ♀ (10) 118–124 (av. 121.9 mm.); culmen ♂ (9) 32–34 (av. 32.8 mm.); ♀ (10) 29–31 (av. 30 mm.).

Range.—Camiguin South Island.

Hypothymis azurae

Mayr, 1945, Zoologica, **30**, p. 113; Parkes, 1965, Ann. Carnegie Mus., **38**, pp. 61–62.

The range of this species is from India to Formosa and south through Malaysia to Java, Flores, and the Philippines. There is a geographical representative species, *H. puella* in Celebes, and in the Philippines are two other, very distinct species, endemic, rare, and of limited distribution. In the Philippines, including the Palawan group and Sulus, the subspecies *H. a. azurae* is common and widespread in lowland and mid-altitude forests, and recorded on 30 is-

lands by McGregor. Minor variation in shade of color and extent of pattern have been pointed out by Mayr and Parkes, but not of subspecies rank.

The widespread Philippine subspecies is blue with abdomen and flanks white and with band on forehead, broad patch on nape, and narrow collar on upper breast black. The female differs in having upperparts dull olive brown, breast greyish, and in lacking black marks.

The new collection from Camiguin South yielded eight specimens of this species that indicate a unique population, worthy of subspecies designation.

Hypothymis azurae catarmanensis, new subspecies

Type.—Field Museum of Natural History no. 284513 from Catarman Mountain, 4,950 feet, Catarman, Camiguin South Island, Philippine Islands. Adult female, collected June 20, 1968 by D. S. Rabor.

Diagnosis.—Male like that of *H. a. azurae* in general pattern but with blue parts of plumage deeper and more purplish blue; also black area on nape reduced in size (absent in 1 of 3 specimens). Wing, 70, 73, 75; tail, 69, 76, 77; culmen, 16, 16, 17 mm.

FEMALE (4 of 5 specimens).—Strikingly different from that of *H. a. azurae* in having the back and wings and tail blue, not brown, and in having the throat and breast deeper blue. In effect, these females look like rather dull, paler males, without the black throat band and without the black nape patch. Wing, 71, 71, 73, 76; tail, 68, 70, 70, 72; culmen, 16, 16, 17, 17 mm.

FEMALE (1 of 5 specimens).—Like female of *H. a. azurae* but part of back with a bluish tinge (not olive brown), upper wing coverts blackish, glossed purplish blue (not brownish) and outer edges of wing quills and tail quills with a bluish tinge (not brownish). (On immature plumage only?) Wing, 74; tail, 72; culmen, 16 mm.

Wing length from various localities:

H. a. azurae

Negros	♂ 68–74	♀ 67–70 mm.
Siquijor	♂ 72–75	♀ 70–73
Bohol	♂ 67, 69, 70	♀ 66–68
Samar	♂ 65–70	♀ 63–68
Mindanao	♂ 67–70	♀ 64–69

H. a. catarmanensis

Camiguin South ♂ 70–75 ♀ 71–76 mm.

Range.—Camiguin South; lowlands to 4,950 feet on peak of Mount Camiguin.

Remarks.—For comparison we have large series of *H. a. azurae* from Luzon, Negros, and Mindanao, moderate series from Palawan, Bohol, Siquijor, Samar, Cebu, and one or a few specimens from each of Polillo, Sibuyan, Romblon, Mindoro, Guimaras, and Basilan. Males and females are about equally represented in all these series, every blue-backed bird has the black nape patch, usually of considerably greater extent than in that of the Camiguin South birds with the largest patch. The size of the black throat band is variable, rarely absent. All the females have brown backs (of various shades of brown or greyish-brown).

There is always a possibility of some mis-sexing of specimens in the field, but the blue-backed females from Camiguin South are not like any specimens, male or female, from any other islands.

The following tentative conclusions are advanced.

There is a reduction in sexual dimorphism through the female becoming partly cock-feathered, notably in the blue back, and the male becoming more like this new type female through the partial loss of the black nape patch.

There is an indication, from this collection, that the female may be dimorphic, most (4 out of 5) are much like dull males but without black markings; a few (1 out of 5) are more like the female of *H. a. azurae*. However, this may be an earlier plumage, special to the immature female in this population.

There are two other species of the genus in Philippines: *H. helenae*, Camiguin North, Luzon (series Field Museum), Samar, Mindanao; and *H. coelestis*, Luzon, Negros, Sibuyan, Dinagat, Mindanao, Basilan; and neither is known to occur on Camiguin South. One may be tempted to consider the possibility that this absence has allowed sexual dimorphism to decrease. But, there are other islands in the Philippines, with only *H. azurae*; and over most of the range of *H. azurae* it is the only representative of the genus. Birds from Nepal have the same male and female mode of plumage as do those of *H. a. azurae* of Philippines.

Dicaeum trigonostigma

Salomonsen, 1960, Amer. Mus. Novit., No. 1991, pp. 28–37.

This is a widespread species presumably originating in the Philippines (though absent from Palawan) where Salomonsen recognized nine subspecies, most of them with striking and clear-cut characters. In all the rest of the range (Java and Borneo to Assam), only five subspecies have developed and most of them with rather trivial characters. Five of the nine subspecies recognized in the Philippines are small island subspecies: on Romblon and Tablas (*intermedium*); Sibuyan (*sibuyanicum*); Siquijor (*besti*); Jolo, Tawi-tawi, Siasi (*assimile*); and Sibutu (*sibutuense*). An additional subspecies proves to have been developed on Camiguin South, raising the number of Philippine subspecies to ten, and six of them small island subspecies.

The near relatives of the Camiguin South form seem to be the geographically adjacent *cinereigularae* of Mindanao–Samar–Leyte–Bohol area, and *besti* of Siquijor, and it is with these that comparison is needed, differing as they do chiefly in color of chin and throat, and in size.

Dicaeum trigonostigma besti Steere

Diagnosis.—Male, chin and upper throat yellow; rest of throat and sides of neck uniform grey, without a yellow wash. Size, small. Male, wing (10), 50–53 (av. 51.8 mm.); culmen (10), 13–14 (av. 13.3 mm.).

Dicaeum trigonostigma cinereigulare Tweeddale

Diagnosis.—Male, chin and upper throat yellow; lower throat and side of neck grey washed with yellow. Size, small.

	wing	culmen
Samar, male	(10) 50–52 (av. 51)	(10) 11–13.5 (av. 12.4)
Bohol, male	(4) 49–52 (av. 50)	(4) 12–13 (av. 12.5)
Mindanao, male	(10) 49–52 (av. 51.2)	(10) 12–13.5 (av. 12.7)

Dicaeum trigonostigma isidroi, new subspecies[1]

Type.—Field Museum of Natural History no. 284521 from Kasangsangan, Catarman, Camiguin South Island, Philippine Islands. Adult male collected June 11, 1968, by D. S. Rabor.

Diagnosis.—Like both of the above subspecies but differs in the male having the chin and upper throat much paler yellow; in having

[1] This new race is named in honor of Dr. Antonio Isidro, president of Mindanao State University, and in appreciation of his great interest in biological research.

the lower throat pale, whitish grey (without any yellowish wash) becoming darker toward the sides of the throat; size larger. Wing ♂ (10), 55–57 (av. 55.6 mm.); culmen (10), 13.5–15 (av. 14 mm.).

Range.—Camiguin South Island, 1,000–2,500 feet altitude.

Remarks.—Most races of this species in Philippines have wing 48–53 mm.; but there are two larger subspecies, the present one (see above) and *sibuyanicum* wing 54–57 mm., both small island species.

Zosterops nigrorum

Mees, 1957, Zool. Verh. Rijk. Mus. Nat. Hist. Leiden, No. 35, pp. 160–170; Mayr, 1967, Peter's Check-list of Birds of the World, **12**, pp. 299, 300.

This is the only species of *Zosterops* in the Philippines that has completely yellow underparts. It is a species of large and small islands: large islands in the north, and the western central islands—Luzon, Mindoro, Masbate, Panay, and Negros; a very few scattered small islands—Camiguin North (north of Luzon); and a few small islands in the central Philippines with southern outposts on Cagayancillo (west of Negros, in Sulu Sea) and Camiguin South in Mindanao Sea.

The relationships of this species are not clear, but the general appearance of the various subspecies, and their differences from other species, in appearance and range, seem to indicate a natural group, forming an endemic Philippine species, as treated in recent revisions.

Up until now the known ranges of the related *everetti*, with underparts partly grey or white as well as yellow, and *nigrorum* have been allopatric. However, on Camiguin South Rabor found both species, *everetti* at low altitudes and *nigrorum* at higher altitudes. This is the only locality where both species occur. (It may be recalled that the old records of *Z. everetti siquijorensis* for Negros are in error, surely due to a mis-identification of specimens of *Z. montana pectoralis*.)

Seven subspecies of *Z. nigrorum* are recognized in the following, and are arranged in three groups.

Group I.—Four races, generally bright to moderately bright in coloration; eye ring complete; little or no black or dusky in side of head; size smaller; wing ♂ 50–56 mm.

Zosterops nigrorum meyleri McGregor

Range.—Camiguin North.

Diagnosis.—A small race, separable from all other races by wide, complete eye ring, especially wide below the eye, according to Mees

whose scant material was variable in color. His pen and ink drawing of head indicates a short dusky streak below white eye ring only.

McGregor, 1908, Manual Philippine Birds, pp. 618–619, says this race is similar to *richmondi* but lacks the black under eye and has eye ring wider.

Wing (4), 53.5–56 (av. 54.4); culmen (4), 12.8–13.8 (av. 13.2 mm.). (Mees) no specimens seen.

Zosterops nigrorum aureiloris Ogilvie Grant

Range.—Northwestern Luzon, south certainly to Mountain and Abra Provinces and Benguet; farther south intergradation with the next two races to be expected; also on Mindoro; sea level to 5,000 feet.

Diagnosis.—A small, brightly colored race, complete eye ring, with, at most, a dusky smudge below it; loral area and a narrow area on forehead golden yellow and sharply contrasting with rest of upperparts; upperparts bright yellowish olive green; underparts bright yellow with flanks lightly tinged olive.

Male, wing (10), 49–56 (av. 53.0); culmen (10), 11–13.5 (av. 12.3 mm.).

Remarks.—Series from Ilocos Norte, Abra, and Mountain provinces. Collected by Rabor, in Field Museum of Natural History.

Zosterops nigrorum sierramadrensis new subspecies

Type.—Field Museum of Natural History no. 259880 from Luzon Island, Cagayan Province, Gonzaga, Mt. Cagua (in the Sierra Madre), 2,000–4,000 feet altitude. Adult male collected April 30, 1960.

Diagnosis.—Like *aureiloris* of northwestern Luzon, but upperparts darker, less yellowish, forehead darker yellow usually with an ochraceous tinge; underparts deeper yellow on the throat, and with more of an olive wash on breast and flanks; bill slightly longer. Thus, a more intensely colored, darker race.

Wing ♂ (10), 50–54 (av. 51.2 mm.); culmen (10), 12–14 (av. 13.1 mm.).

Range.—Northeastern Luzon in Cagayan Province. Presumably ranges southward to intergrade with the next race in central Luzon.

Remarks.—Series from Cagayan Province in Field Museum of Natural History. This is an additional example of northwestern and northeastern Luzon birds representing different subspecies, as

discovered by Dr. Rabor's field work in 1959 and 1960. (See Rand and Rabor, 1967, *Fieldiana:* Zool., **51**, pp. 85–89.)

The moderately well-marked characters of this new race show very plainly in series, and there is little trouble in allocating most individual male specimens from Ilocos Norte Mountain and Abra specimens on the one hand, and Cagayan specimens on the other. Females are duller.

The earlier lack of recognition of this northeastern subspecies was due to lack of adequate material, and there is the probability that central Luzon, easily reached by collectors, may be where three subspecies merge.

Zosterops nigrorum luzonica Ogilvie Grant

Range.—Southern Luzon; probably meeting and intergrading with the above two races in central Luzon.

Diagnosis.—Like *sierramadrensis* but differs most notably in the much less, and paler yellow in the forehead and lores. There is also a better developed dark line below the eye ring and average slightly richer yellow below, and a slightly clearer green above.

Wing ♂ (10), 50–56 (av. 52.8); culmen ♂ (10), 13–14 (av. 13.3 mm.).

Remarks.—Series from Camarines Sur and Sorsogon of extreme southern Luzon.

Again, material has been scarce in collections from southern Luzon. For example, in 1957 Mees had seen but two specimens.

Group II.—One race; dull; eye ring interrupted by black spot in front; black line in lower lores—below eye ring area definite and distinct; size medium, wing, ♂ 54–58 mm.; culmen, 13–14 mm.

Zosterops nigrorum nigrorum

Range.—Masbate, Caluya, Ticao, Cresta de Gallo, Panay, Negros.

Diagnosis.—Differs from all three Luzon races in the white eye ring being interrupted in front by a black spot and the black line below the eye ring being better developed, in the underparts being much colder, duller yellow and the much more extensive and heavier greyish olive wash over breast and sides of body; size slightly larger.

Wing ♂ (10), 54–58 (av. 55.6); culmen (10), 13–14 (av. 13.6 mm.).

Remarks.—Field Museum of Natural History has a good series of Negros birds (Rabor collection). Mees (loc. cit., p. 164) found no

differences between populations from Negros, Panay, and Masbate. Field Museum also has two specimens from Ticao (McGregor and Celestino collection) which agree with Negros birds on the main characters, although differ somewhat in shade of general coloration. Wing, ♂ 58, ♀ 57 mm.; culmen, 13–14 mm.

The habitat on Negros is the rain forest and second growth.

GROUP III.—Two races, bright, eye ring incomplete, interrupted by black spot in front; black below eye ring distinct; size larger; wing, 57–62 mm.; culmen, 14–16 mm.

Zosterops nigrorum richmondi McGregor, 1904

Range.—Cagayancillo Island (Cagayan Islands), in the Sulu Sea.

Diagnosis.—Like *nigrorum* in the pattern of the side of the head with black spot interrupting eye ring in front and confluent with the distinct black line below lores and eye ring. Differs from *nigrorum* in larger size, in upperparts much lighter and more yellow green; in whole underparts being much brighter more intense yellow, with reduced olive tinge in flanks.

Wing, ♂ 58, ♀ 59; culmen, 15, 15 mm.

Remarks.—Known only from Cagayancillo (now called Cagayan), the largest (5 miles by 1 mile) island of the Cagayanes group west of Negros and about 70 miles southwest of Panay, the nearest island. The habitat is described by McGregor, 1904, Bull. Phil. Mus., No. 3, p. 5: the island reaches several hundred feet altitude: surface, coral rock; vegetation scanty, coconut palms along shore, occasional mangoes, small clumps of bamboo, some mangrove, various shrubbery, trees, masses of rank grass and tall weeds; no streams, little marsh. This *Zosterops* was very common throughout.

Zosterops nigrorum catarmanensis new subspecies

Type.—Field Museum of Natural History no. 284585 from Catarman Mountain, Catarman, Camiguin South Island; 2,000–4,500 feet altitude. Adult male collected June 20, 1968 by D. S. Rabor.

Diagnosis.—Like *nigrorum* and *richmondi* in having the white eye ring interrupted anteriorly by a black spot confluent with the black line below lores and eye ring; like *richmondi* in large size; differs from *richmondi* in the brighter, clearer green of upperparts; in yellow of super-loral being clearer, brighter yellow, and in yellow of underparts being much brighter and clearer.

Male, wing (7), 57–62 (av. 60); culmen (6), 14–16 (av. 14.6 mm.).

Range.—Camiguin South in Mindanao Sea, between 2,000 and 5,700 feet altitude.

Remarks.—In the yellow of the underparts *catarmanensis* is very similar to *aureiloris* of northeastern Luzon, although the green of the upperparts is slightly brighter, clearer green; and, of course, there is the difference in size and in the loral area.

FIELDIANA · ZOOLOGY

Volume 51 | MAY 25, 1970 | No. 14

A New Species of Frog of the Genus *Rana* from Thailand

ROBERT F. INGER
CHAIRMAN, SCIENTIFIC PROGRAMS

Two adult frogs, a male and a female, clearly belonging to the ranae liebigianae group of Boulenger (1920) were collected several years ago in Chantaburi Province, Thailand. They constitute the first Thai record of this species group, which is mainly if not exclusively a group adapted to life in swift streams (Liu, 1950; Bourret, 1941), usually in montane areas. All have extensively webbed toes, the tips of the digits more or less swollen, depressed heads, and stout legs, and the males of most species have melanic, cornified spines at least on the inner fingers and chest. They lack the odontoids of the mandible characteristic of the ranae kuhlianae and ranae grunnientes groups, the other groups of the subgenus *Rana* from tropical Asia having fully webbed toes and the tips of the digits swollen.

The Thai sample appears to represent a new species distinguished by several characters and separated from the nearest known related population (*Rana verrucospinosa* Bourret) at Bach Ma, South Viet Nam, by a distance of 700 km. Its most distinctive feature is the grouping of ventral spines in the male into small bundles, hence the specific name.

Rana fasciculispina, sp. nov.

Holotype.—An adult male from Kao Soi Dao, Changwat Chantaburi, Thailand, collected July 5, 1961 by Mr. Boonak. National Center for Reference Collections of Thailand, number 513-1385.

Diagnosis.—A large member of the ranae liebigianae group of Boulenger; webbing complete, not emarginate; tips of toes swollen to twice width of phalanges; proximal subarticular tubercles of fingers twice as long as distal ones (Fig. 1); back (Fig. 2) with numerous short, thick ridges, none as long as diameter of eye, interspersed with circular warts; male with ventral spines in groups of 5–10 (Fig. 3), clusters distributed across chest and throat.

Library of Congress Catalog Card Number: 74-122685

Publication 1096

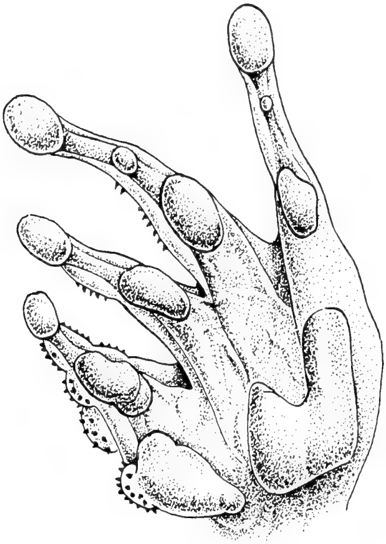


FIG. 1. Ventral surface of hand of male holotype of *Rana fasciculispina*, sp. nov.

Description of holotype.—Habitus robust; limbs heavy but long; head as wide as long; snout obtusely pointed, shorter than eye; nostrils midway between eye and tip of snout; canthus obtuse; lores oblique, weakly concave; interorbital narrower than upper eyelid; tympanum visible but obscure, about two-fifths eye diameter; distance between eye and tympanum about twice diameter of tympanum; vomerine teeth in short, slightly oblique groups between and just behind choanae, separation of groups shorter than their distance from choanae.

Tips of fingers distinctly swollen; first longer than second; both margins of second and third fingers with narrow fringes of skin; subarticulate tubercles conspicuous, proximal ones elongate and twice length of distal ones on third and fourth fingers; prepollex projecting strongly, but not extending beyond base of proximal subarticular tubercle of first finger.

Tips of toes swollen into round disks twice width of phalanges; all toes completely webbed to disks, web not emarginate; subarticular tubercles prominent, proximal ones elongate but not as long as those of fingers; inner metatarsal tubercle not compressed, length about

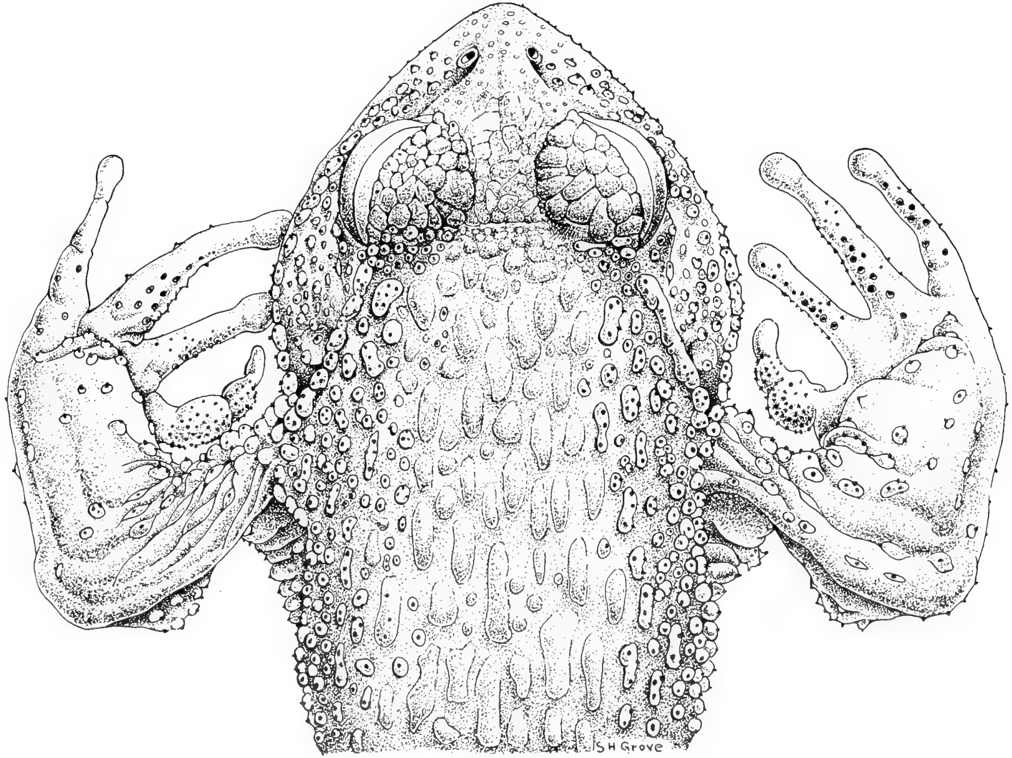


FIG. 2. Dorsal view of anterior half of male holotype of *Rana fasciculispina*, sp. nov.

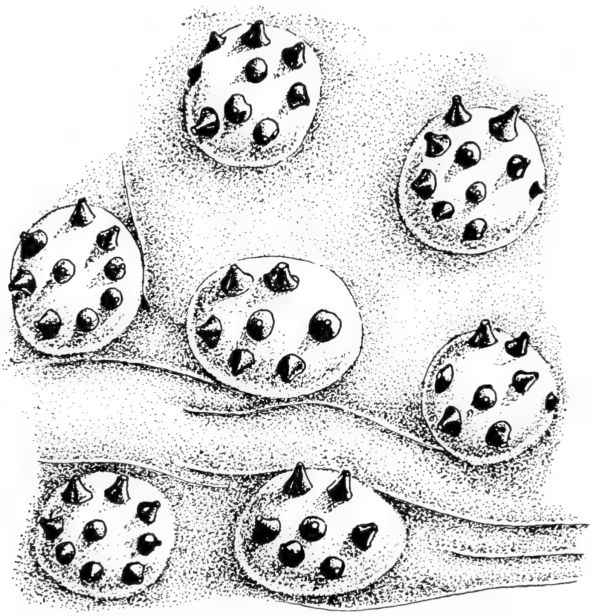


FIG. 3. Clusters of spines in mid-pectoral region of male holotype of *Rana fasciculispina*, sp. nov.

60 per cent length of first toe; no outer metatarsal tubercle; first and fifth toes with flaps of skin; an obscure, short tarsal ridge.

Back with numerous short, thick ridges, none as long as diameter of eye, interspersed with numerous circular warts; eyelids with circular tubercles; forehead smooth; sides of head and body with round warts; dorsal surfaces of limbs with round tuberosities mostly arranged in longitudinal series; ventral surfaces smooth except for secondary sex characters.

Male with circular vocal sac openings in floor of mouth; forearm enlarged; inner surface of forearm, entire chest, and throat with circular whitish tubercles each bearing 5 to 10 strong black spines; dorsal surface of prepollex and first finger with strong black spines not grouped into circular clusters, spines of prepollex separated from those of first finger by an area of smooth skin; dorsal surfaces of second, third, and fourth fingers with black spines; density and size of spines decreasing from first to fourth fingers; one to six black spines on warts and tubercles of sides of head and body; warts and ridges of back generally free of spines.

Color in preservative brownish with obscure darker spots on back.

Paratype.—Field Museum of Natural History 171309, an adult female collected at same time and place as holotype. The paratype contains a few enlarged, non-pigmented ova. It agrees in most respects with the holotype except in the secondary sex characters. The ridges on the back are not as elevated as those of the male, while the dorsal spotting is more conspicuous.

Measurements (in millimeters)	Holotype	Paratype
Snout-vent	106	104
Head width	43	41
Head length	42	40
Diameter of tympanum	4	4
Diameter of eye	14	14
Eye-tympanum distance	8	7
Interorbital width	7	7
Width of upper eyelid	9	10
Tibia	53	49

Comparisons.—*Rana fasciculispina* differs from all previously described species of *Rana* in the grouping of the ventral spines into small clusters distributed across the breast in the male. In other members of the ranae liebigianae group the spines are single, whether spread across the chest or restricted to its lateral portions (see Boulenger, 1920). In two characters, *R. fasciculispina* differs from all other species of the ranae liebigianae group except *R. mediolineata* Bourret: (1) The tips of the toes are swollen to twice the width of the phalanges. In other species of this group, the tips of the toes are either not (e.g., *phrynoides*) or only slightly (e.g., *boulengeri, spinosa*) wider than the phalanges. (2) The proximal subarticular tubercles are elongate and those of the fingers are at least twice the length of the distal ones. In the other species the proximal subarticular tubercles are either circular or not much longer than the distal ones.

Rana fasciculispina differs from *mediolineata* and resembles *spinosa* and *boulengeri* in the sculpturing of the dorsal skin. In *mediolineata,* according to the original description and figures (Bourret, 1937), the ridges of the back and sides are very narrow and a number of them are longer than the diameter of the eye. In contrast, the ridges of *fasciculispina, spinosa,* and *boulengeri* are thick and none is as long as the eye; they resemble the dorsal ridges of *verrucospisona* figured by Bourret (1937).

Remarks.—The large, non-pigmented ova of the paratype of *R. fasciculispina* indicates that this species probably oviposits under large rocks in swift streams as does *R. boulengeri* (Liu, 1950).

The area of distribution of this species group lies more than 1,000 km. north of the type locality of *R. fasciculispina*. The group is known from South and Southwestern China (*phrynoides, spinosa, yunnanensis, boulengeri*), northern India and Sikkim (*liebigi, gammei, annadalei*), northern Burma (*feae*), and North Viet Nam north of 21°N (*yunnanensis, verrucospinosa, spinosa, phrynoides,* and *mediolineata*). Only one previously recorded locality, at Bach Ma (16°30′N), South Viet Nam (Bourret, 1941), for a species of this group lies south of the main range.

The Thai locality is in a small range of low mountains separated by about 50 km. from another range that runs northward toward Laos and eastward along the Thai-Cambodian border before turning northward again toward Laos and northern Viet Nam. Presumably, the species group has used these montane corridors to reach southeastern Thailand. Probably additional undiscovered populations exist in the streams of these mountains in Thailand and Laos.

Acknowledgements.—I am grateful to Dr. Prasert Lohavanijaya and Mr. Noel Kobayashi, National Center for Reference Collections of Thailand, for the privilege of describing these animals and for many kindnesses shown me in Thailand.

REFERENCES

BOULENGER, G. A.

1920. A monograph of the South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana*. Rec. Indian Mus., **20**: 1-226.

BOURRET, RENÉ

1937. Notes herpétologiques sur l'Indochine française. xiv. Les batraciens de la Collection du Laboratoire des Sciences naturelles de l'Université. Bull. Gén. Instr. Pub. Hanoi, 1937, 1-56.

1941. Les batraciens de l'Indochine. Inst. Océanogr. Indochine, pp. 1-547.

LIU, C. C.

1950. Amphibians of Western China. Fieldiana: Zool. Mem., **2**: 1-400.

FIELDIANA • ZOOLOGY

Volume 51 JUNE 5, 1970 No. 15

Notes on land slugs, 16[1]: *Deroceras* from Afghanistan, including description of *D. kandaharensis*

C. O. VAN REGTEREN ALTENA
RIJKSMUSEUM VAN NATUURLIJKE HISTORIE, LEIDEN, NETHERLANDS

Among mollusks collected by members of the W. S. and J. K. Street Expedition to Afghanistan in 1965 were 47 specimens of land slugs belonging to the genus *Deroceras*. Through the kindness of Dr. Alan Solem, Curator of Lower Invertebrates, Field Museum of Natural History, it was possible to study this material and to retain a few examples for the Rijksmuseum van Natuurlijke Historie, Leiden. I am indebted to Mr. E. Gittenberger for preparation of a radular mount; to Mr. W. C. G. Gertenaar for assistance with the illustrations, and to Dr. Solem for correcting the translation.

Previously Likharev and Starobogatov (1967) reported *Deroceras laeve* (Müller, 1774) from near Kabul. Most of the Street Expedition material was taken in the same area and is referred to this species. One set from near Kandahar consisted of both *D. laeve* and a new species that is described below as *Deroceras kandaharensis*. Although it was collected from cultivated gardens, I do not consider that it is an introduced species.

Deroceras kandaharensis new species. Figure 1, *a–e*.

Diagnosis.—A species of *Deroceras* with white line on the dorsum continuing into the posterior keel, ovotestis extending from caecum to end of cavity, oviduct narrow at first, then turns sharply before widening, penis lacking appendix and internally with a stimulator having a peculiar white cap.

Deroceras buchar (Simroth, 1910) is the most similar species, but is distinctly smaller, sometimes lacks an intestinal caecum, lacks the

[1] 1969. Notes sur les limaces, 15: Quelques limaces d'Israël, *in* Basteria, 33, (1–4), pp. 3–10, 18 figs.

Library of Congress Catalog Card Number: 72–124483

Publication 1099

white dorsal coloration, and does not have the sharply-reflexed oviduct. No other species are immediately comparable.

Description.—Color yellowish white with some grey pigmentation on mantle. Dorsum with white line in middle that on posterior half edges an increasingly prominent keel (fig. 1, *a*). Pigmentation heaviest on sides of keel; neck and sole nearly white.

Radula of holotype with 88 rows of denticles, formula at right side of thirtieth row from posterior margin, 1–16–28. Form of denticles typical of genus.

Intestine poorly preserved, but caecum agreeing with that of *D. reticulatum* seen in two dissected examples. Other features of intestine agreeing with generic definition.

Ovotestis very large, extending from level of intestinal caecum to posterior end of body cavity. Hermaphroditic duct somewhat sinuated, albumen gland (fig. 1, *b*) relatively small. Spermoviduct for first 8 mm. large, then for next 5 mm. about as thin as prostate. Vas deferens short, entering penis lateral to insertion of penial retractor muscle. Free oviduct narrow at first, sharply reflexed, broadening (fig. 1, *c*) before entering atrium. Penis oval, without appendix, broader below middle, narrowing abruptly before entering atrium. Seminal receptacle globular, with short and narrow shaft that inserts on lower portion of penis, just before latter narrows. Atrium short, without unusual features.

Interior of penis (fig. 1, *d*) with a large stimulatory papilla surmounted by a small "dunce's cap" (fig. 1, *e*) that is soft and white except where some tissue connects to it.

Length of holotype 30 mm., mantle length 11.5 mm.

Holotype.—Afghanistan: cultivated gardens of Baba Wali near Kandahar, 1,425 m., Kandahar Province, 31° 36′ N, 65° 47′ E. Collected by the Street Expedition on November 9, 1965. Field Museum of Natural History (FMNH) number 151672.

Paratypes.—FMNH 147120 and Rijksmuseum, Leiden, 4 specimens.

Remarks.—All of the specimens were between 25 and 30 mm. in length. There was little variation in color, none of the examples being dark, but some showing practically no pigmentation. Two dissected specimens showed the intestinal caecum, and three individuals showed the peculiar "dunce's cap" on the penial stimulator. Two of these had the cap smaller and less clearly formed than in the holotype. Possibly this may be lost during copulation and a new cap

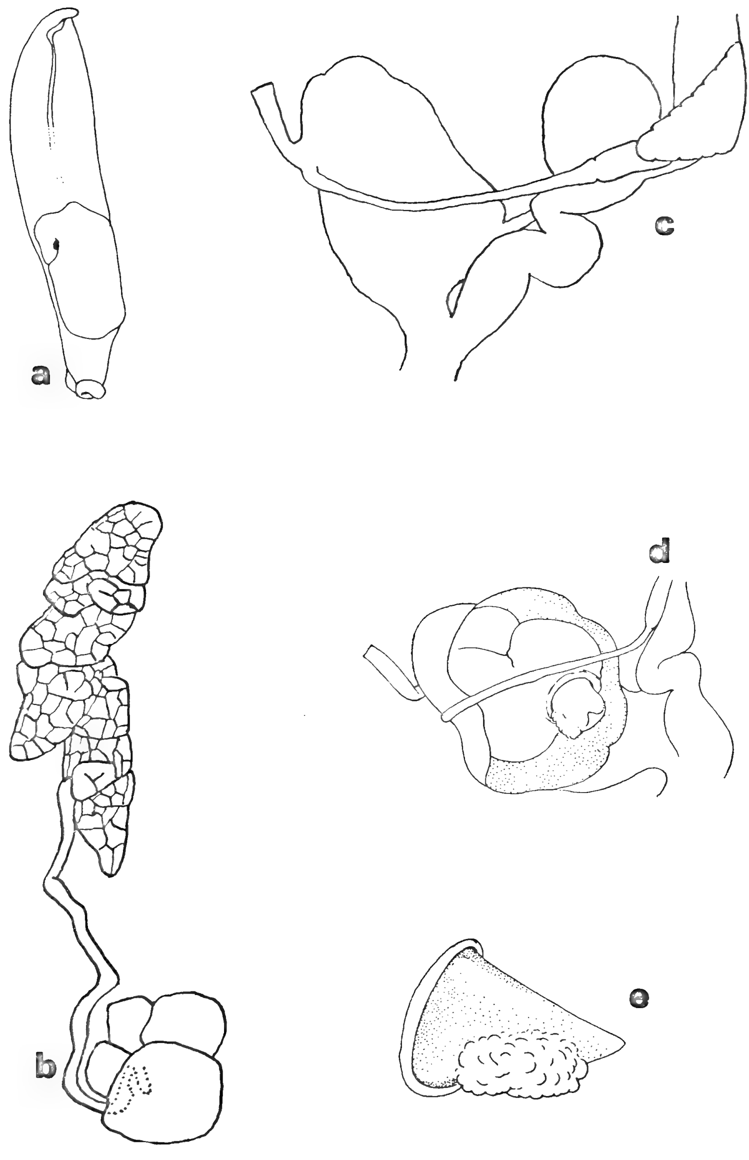


FIG. 1. *Deroceras kandaharensis* new species. *a*, Dorsal view of a paratype (2 ×); *b*, ovotestis, hermaphroditic duct, talon, and albumen gland of holotype (5 ×); *c*, terminal genitalia of holotype (10 ×) showing insertions of vas deferens, penial retractor muscle, spermatheca, and shape of oviduct; *d*, interior of penis from holotype (10 ×) showing stimulatory papilla and "cap"; *e*, "dunce's cap" structure on stimulatory papilla (20 ×) from dissected holotype.

formed subsequently, although its solid attachment to the stimulator does not make this very likely.

Deroceras buchar (Simroth, 1910, pp. 523–526, 558–560, pl. VII, figs. 19–21) is known from a fragmentary description and penial illustrations showing little detail. I hesitated whether to refer this material to Simroth's species, but several features present in the Afghanistan specimens would not have been overlooked by Simroth. The white dorsal line, reflexed oviduct, and very large ovotestis are characters that are readily visible even in poorly preserved material. Simroth notes the same kinds of characters in descriptions of other slug species. His failure to do so in reference to *D. buchar* is interpreted as meaning that these characters were not present in specimens of that taxon. Since in reference to other limacid slugs these types of differences have been shown to denote specific separation, I am describing the Kandahar specimens as a new species. *D. buchar* was reported from several localities between the Caspian Sea and Fergana. The intestinal caecum and the penis look similar to that of *D. kandaharensis*, but too little detail is shown for meaningful comparisons. Most other *Deroceras* show obvious differences in having, for instance, penial appendices.

Deroceras laeve (Müller, 1774)

Material.—Highly irrigated area at 2,240 m. elevation near Paghman, Kabul Prov., Afghanistan, 34° 36′ N, 68° 56′ E, collected August 23, 1965 (32 specimens, FMNH 147081, FMNH 147082, Rijksmuseum, Leiden); cultivated gardens of Baba Wali, 1,425 m., Kandahar, Kandahar Prov., Afghanistan, 31° 36′ N, 65° 47′ E, collected November 9, 1965 (10 specimens, FMNH 151673).

Remarks.—Five of the 32 specimens from Paghman were dissected. Of these, three were aphallic, the other two with typical penial structure. Size of the entire set varied between 10 and 23 mm. in body length. The 10 specimens from Kandahar were 10 to 21 mm. long, with all four dissected examples aphallic.

Literature Cited

Likharev, I. M. and Y. I. Starobogatov

1967. On the molluscan fauna of Afghanistan, *in* Trudy Zool. Inst., Akad. Nauk SSSR, **42**, pp. 159–197, 19 figs.

Simroth, H.

1910. Kaukasische und asiatische Limaciden und Raublungenschnecken. Ann. Musée Zool. Acad. Impériale Sci. St.-Pétersbourg, **15**, pp. 499–560, pls. VI–VIII.

FIELDIANA · ZOOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 51 FEBRUARY 20, 1970 No. 15

Morphological Parallelisms of the Bulla and Auditory Ossicles in Some Insectivores and Marsupials

WALTER SEGALL
RESEARCH ASSOCIATE, VERTEBRATE ANATOMY

ABSTRACT

Insectivores and marsupials show similar phylogenetic stages of morphological differentiation of the tympanic, entotympanic, and the malleus, which range from generalized (*Solenodon–Didelphis*) to the highly specialized (*Tupaia–Dromiciops*). In the insectivores the tympanic process of the basisphenoid takes the place of the tympanic process of the alisphenoid of the marsupials. The presence of an entotympanic suggests specialization in both orders. The malleus of marsupials and insectivores undergoes greater morphological changes than the incus. The ossicular functional axis meets the horizontal in a large angle in the generalized taxa and shows a smaller angle and even a negative one in *Dromiciops* and the burrowing insectivores. Apparently, the malleus turned first, as was also shown for marsupials (Segall, 1969b), other morphological changes followed later. This morphological sequence is probably caused by mechanical influences.

In insectivores the stapes is characteristically and consistently specialized, unlike the two other ossicles, which show far greater differences. The marsupials show a greater range in the shape of the stapes, especially of the plate. Even if the stapes is not preserved, as is usually true in fossil specimens, the fenestra ovalis gives an accurate outline of the shape of the stapes plate and of its position. The shape of the latter or the fenestra ovalis in marsupials varies from practically round to oval in the more generalized and elliptical in the specialized taxa. In the insectivores generalized and specialized genera alike have stapes with elliptical plates.

In the fossorial genera of both orders tympanic, malleus, incus, and the articulation between the latter two are markedly affected. However, the stapes retains the ordinal characteristics.

The stapes of the insectivores has well-curved crura. In most genera the stapedial artery fills only a part of the intracrural space, which speaks for the independence of the two. Thus, it can be assumed that the function of the stapes is the most influential factor for determining its shape.

The round outline of the stapes plate (or fenestra ovalis) is considered the primitive condition, the elliptical the specialized one.

Library of Congress Catalog Card Number: 77-115191

No. 1086

INTRODUCTION

This is a continuation of my study of the auditory region of mammalia. The previous report deals with the morphology of the bulla, malleus, and incus in marsupials (Segall, 1969b). This study covers the same aspects of the auditory region in insectivores. Both orders show many great morphological similarities in the phyletic stages of the auditory region and some differences. While in the paper on the marsupials only the malleus, incus, and bulla were considered, in this study special attention is also given to the stapes. The stapes, or in fossils in which the stapes is commonly missing, the fenestra ovalis, may be useful in classification. Since the comparisons between the stapes of insectivores and marsupials led to interesting results, a detailed study of certain marsupial stapes is also presented to supplement the description by Doran (1877). In several places probable functional relationships were mentioned, but these have not been studied.

METHODS AND MATERIAL

All specimens were examined under a binocular microscope. When necessary, obscuring bone was removed to expose the ossicular chain. The angle of the ossicular functional axis with the Frankfurter horizontal plane was measured.

The ossicular functional axis is an imaginary straight line running from the tip of the short crus incudis through the incudo-malleolar joint to the upper insertion of the anterior process of the caput mallei.

The lever ratio has been determined and noted in some specimens. It is the length of the malleolar arm divided by the incudal lever arm. The position and the length of the manubrium and long crus incudis are, therefore, of importance for the function of the auditory system.

The long diameter of the stapedial plate and the maximal width perpendicular to this were measured and the ratio between them determined. Since the stapes plate, with the help of the stapedial ligaments, fits snugly into the fenestra ovalis, the contours of the latter give an exact outline of the plate. Therefore, measurements of the fenestra were taken in specimens lacking the stapes. This provides reliable measurements in fossil material where the ossicle is missing most of the time, but the fenestra ovalis is clearly visible. Measurements of the fenestra ovalis were easier to take and for this reason proved even more exact than the measurements of the stapes ratio based on the stapes in place. The results were repeatedly checked

and small differences were often found. The figures arrived at are, therefore, meaningful approximations.

MATERIAL

The following specimens of the recent and fossil mammal collections of Field Museum of Natural History and the American Museum of Natural History (AMNH) were studied:[1]

Marsupials

Family Didelphidae:
Didelphis 24154, 96199, 13779, 13783, 56196, 15556; *Monodelphis* 70539, 22182; *Marmosa* 61878, 69833, 69845; *Caluromys* 70994, 68801, 22208, 87927; *Philander* 69805, 70983.
Subfamily Microbiotheriinae: *Dromiciops* 50074.

Family Dasyuridae:
Dasyurus 81523, 42759; *Sarcophilus* 46006.

Family Notoryctidae:
Notoryctes 1061 (AMNH).

Family Peramelidae:
Perameles 60943, 64349; *Echymipera* 56369, 56366, 56368.

Family Caenolestidae:
Caenolestes 81464, 70816.

Family Phalangeridae:
Phalanger 53968, 53970; *Petaurus* 64332.

Family Macropodidae:
Macropus 47318, 44295; *Dendrolagus* 60895; *Aepyprymnus* 47429.

Insectivores

Family Solenodontidae:
Solenodon 57207, 18505, 57068, 51068.

Family Nesophontidae:
Nesophontes 17107 (AMNH), 17108 (AMNH).

Family Tenrecidae:
Tenrec 85512, 21846; *Setifer* 85513, 85170; *Echinops* 33948; *Oryzorictes* 05640, 05637, 05641.

[1] I follow in the main Simpson's classification of mammals (1945) for the general level of organization of the forms studied.

Family Potamogalidae:
Potemagale 72831, 25973.

Family Chrysochloridae:
Chrysochloris 26353, 26352.

Family Erinaceidae:
Echinosorex 68736; *Hylomys* 47113, 46336; *Erinaceous* 57525, 82122, 84448; *Hemiechinus* 74549, 41789, 09719.

Family Leptictidae:
Ictops UC1483.

Family Macroscelididae:
Elephantulus 34040, 38494, 38499; *Nasilio* 16659.

Family Soricidae:
Sorex 41788, 41789, 09719; *Blarina* 15284, 44521, 13152.

Family Talpidae:
Talpa 82581, 23519; *Scalopus* 08156; *Scapanus* 09732; *Euroscaptor* 35406; *Condylura* 28783, 80049, 07071, 21707; *Uropsilus* 36143, 36142.

Family Tupaiidae:
Tupaia 63009, 63020, 63018.

MORPHOLOGICAL REMARKS

As is well known, the embryologic and phylogenetic origin of the stapes differs from that of the malleus and incus. The stapes derives from the hyoid arch, while the malleus and incus develop from the mandibular arch. This is supported by the innervation of the muscles of the middle ear. The tensor tympani which inserts into the malleus belongs to the mandibular arch and is innervated by a branch of the trigeminus. The stapedius muscle is derived from the hyoid arch and is innervated by a branch of the facial nerve.

Doran (1877) divides the marsupials into two groups on the basis of the morphology of the stapes. A small group to which, according to him, *Didelphis* and *Macropus* belong have a small opening between the crura, while the rest have a columella-like stapes.

My observations show that not many genera among the marsupials have a columella-like stapes. The majority have a triangular or somewhat triangular stapes with a small opening between the crura. In some genera the opening is pinpoint sized, in others it is

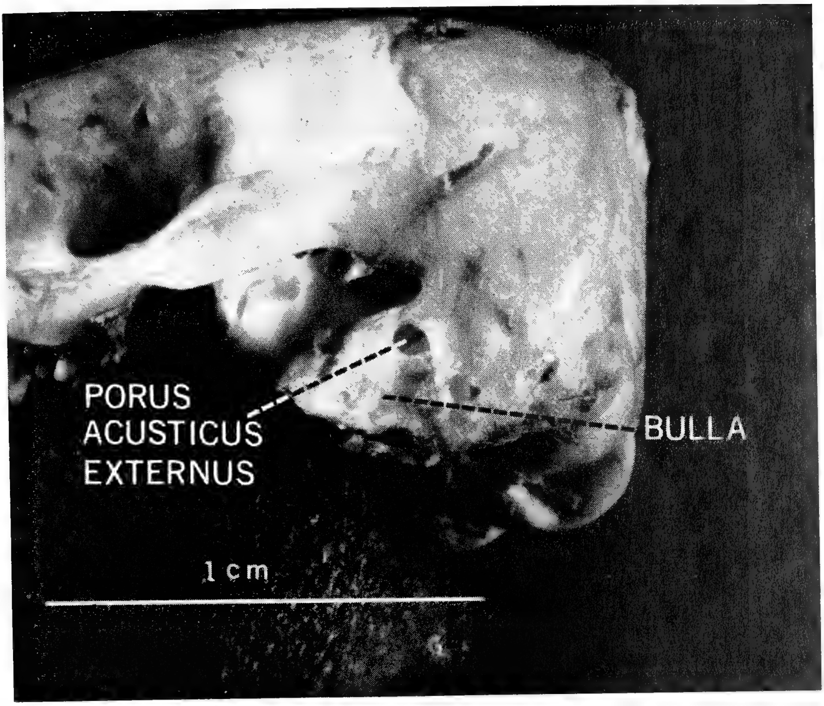


FIG. 1. *Notoryctes typhlops.* Lateral view of the left auditory region.

slightly larger. The term columella-like is used here, although in marsupials the stapes is nowhere near as rod-shaped as it is in monotremes. On cross-section it has an oval (*Dasyurus*) or even flat shape (*Notoryctes*). Toward the base the columella spreads fan-like in the longitudinal diameter of the plate, a condition morphologically intermediate between the columella shape and the typical stirrup of higher mammals. The stapedial plate of the marsupials with a columella-like stapes is about circular or oval. It is more elongated in the various genera and reaches an elliptical shape in the more specialized genera as in *Dromiciops*.

None of the insectivore stapes observed has the columella-like shape, but there is a long elliptical plate in all genera, generalized and specialized alike. Its labyrinthine surface is mostly flat, sometimes convex (*Chrysochloris, Elephantulus*). Its crura are much curved and leave a large opening between them through which the arteria stapedia passes. The latter usually fills one-third to one-half of the linear intracrural space, but very rarely the whole space. Sometimes

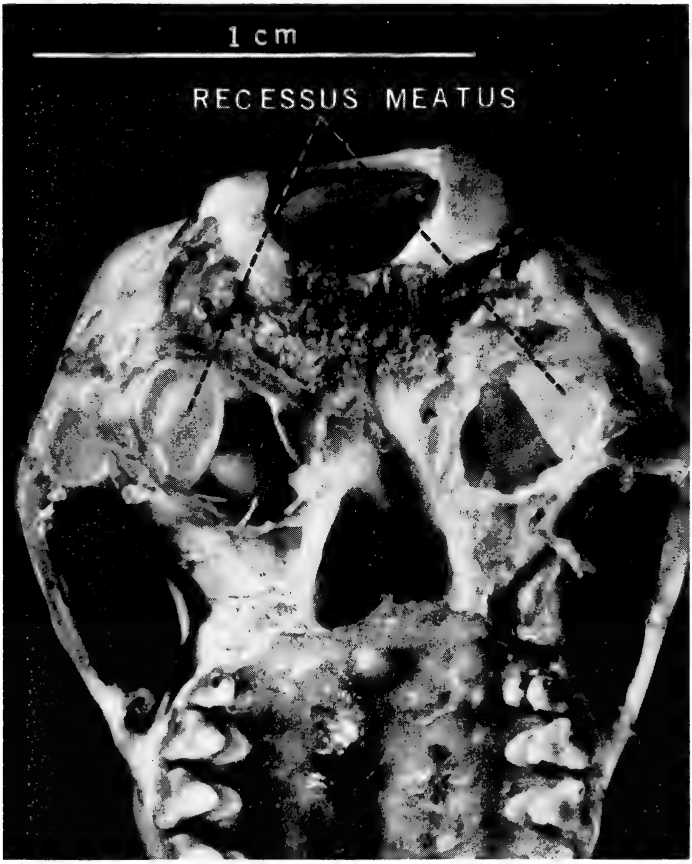


FIG. 2. *Notoryctes typhlops.* Ventral view of the auditory region. (Both bullae broken.)

the artery is enclosed in a bony canal which is sometimes incomplete where the artery passes between the crura (*Chrysochloris, Tupaia*). This condition is found in: *Chrysochloris* (*stuhlmanni* ?) 26352, 26353, *Amblysomus leukorhinus* 81730, *Talpa micrura micrura* 82581, *Scalopus aquaticus* 8151, *Scapanus townsendi* 9732, *Euroscaptor micrura* 35406, *Condylura cristate* 28783, *Tupaia palawanensis* 63009. In all other families studied a bony canal is missing.

Notoryctes typhlops

Figure 1

A description of the relevant parts of the auditory region in *Notoryctes* is included here as a skull was not available to me at the time

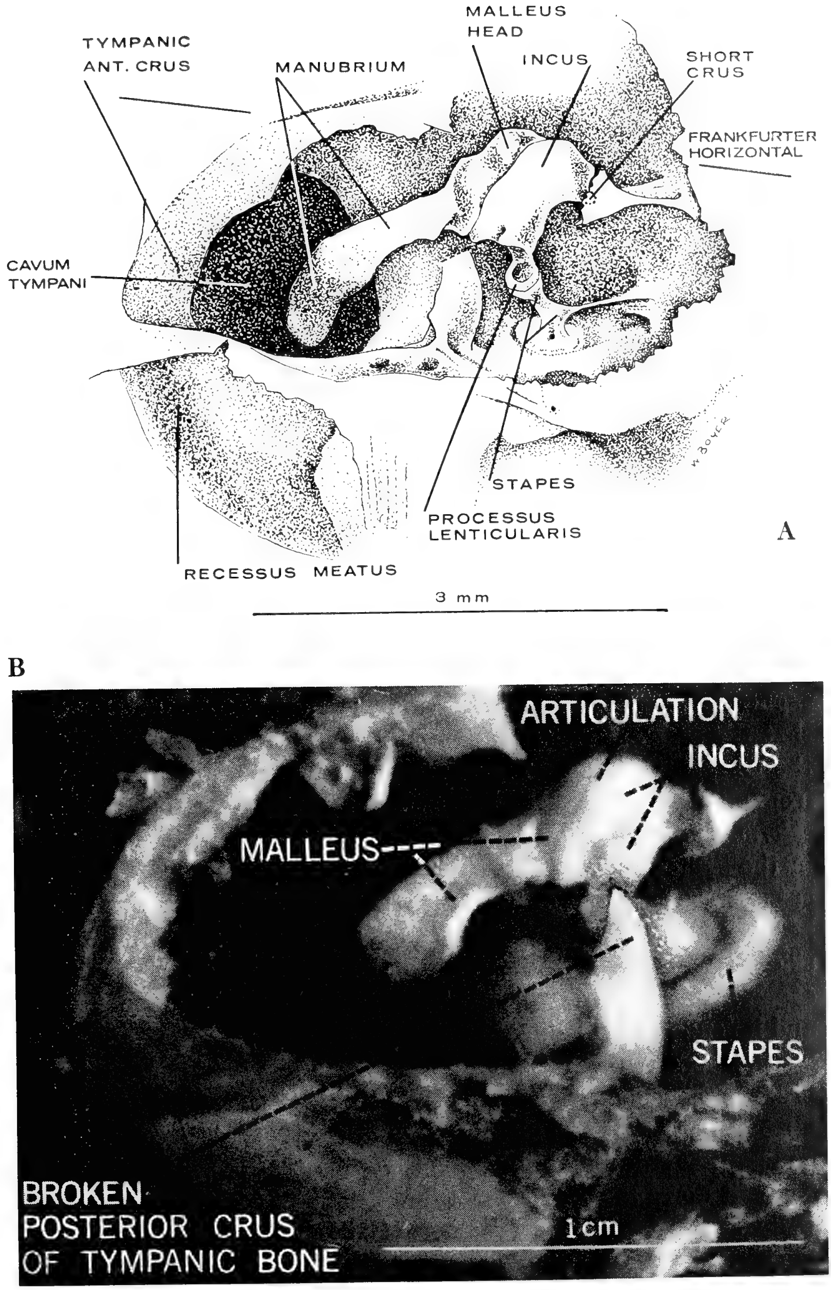


FIG. 3. *Notoryctes typhlops.* A. Lateral view of the left malleus and incus; latero-ventral view of the left stapes. (Obscuring bone removed.) B. Latero-ventral view of left middle ear. (Obscuring bone removed.)

the paper on the auditory region in marsupials was in preparation (Segall, 1969b).

The configuration of the auditory region of *Notoryctes* reminds one very much of that of *Talpa* and *Chrysochloris* (fig. 1). It resembles the latter to such an extent that E. Cope looked upon it not as convergence, but as the result of phylogenetic affinity (Weber, 1928).

A large process of the alisphenoid covers the cavum tympani ventrally. The ectotympanic forms a large recessus meatus which, as in *Dasyurus*, projects into the middle ear (fig. 2). Laterally, the recessus turns in a dorsal direction and forms part of the circumference of the small, oval-shaped porus externus which is similar in appearance to that of *Chrysochloris*. The anterior and posterior crus of the tympanic approach each other closely, leaving a small incisura tympanica open dorso-caudally.

In the specimen studied the ossicles are *in situ* and will be described to the extent that they are visible in that position (fig. 3A, B). No description or illustration of them can be found in the literature.

The shallow head of the malleus is calotte shaped. The line of articulation with the incus is straight and runs from dorsal and slightly caudal to ventral and slightly cranial. It can be assumed that the articulation is even more flat than in the Talpinae and in the Chrysochloridae. The shape of the articulation which differs from all other marsupials, but is similar to that of *Talpa* and *Chrysochloris*, is presumably the result of the modified function of the ossicles in the subterranean genera. A lamina is missing in *Notoryctes*. I suspect the presence of a short neck, although the border between head and neck is ill defined. The manubrium is flat on its lateral side. It has a straight anterior and a somewhat irregular posterior edge. Its distal part, which is slightly wider, is sharply bent medially and its end is rounded.

The body of the incus continues without distinction into the short process, the end of which is pointed and directed caudally. It sits in a small bony cavity which is situated on the edge of a supporting lamina that extends from the medial and posterior wall of the cavity. The flat dorso-lateral part of the stapedial crus incudis is only partially demarcated from the body of the incus by a shallow, short groove. Its delicate, flat, ventro-medial end, which is bent about 90° against the upper part, is slightly concave on its ventral side and articulates through a wide, oval, lenticular process with the identically shaped head of the stapes.

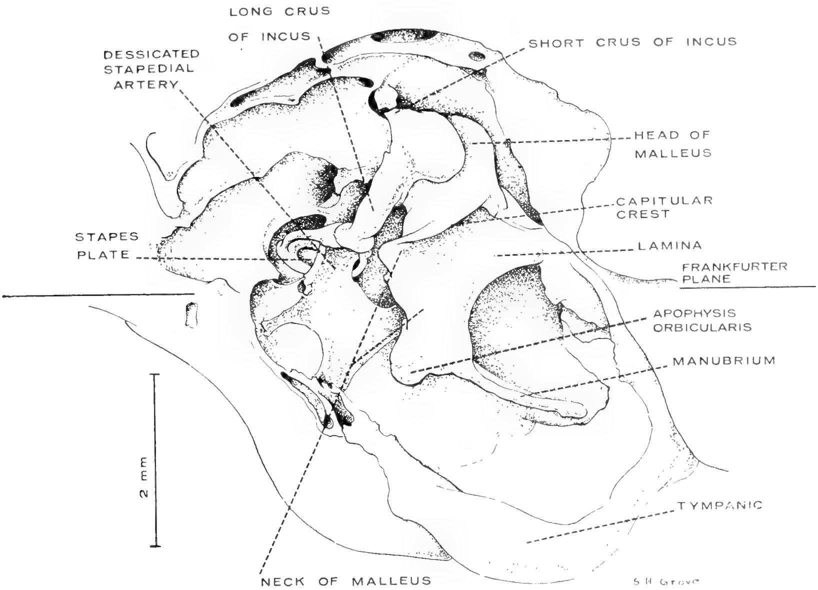


FIG. 4. *Solenodon paradoxus.* Latero-ventral view of right middle ear. (Obscuring bone removed.)

The columella stapedis, which is flat dorso-ventrally, enlarges fan-like in the horizontal plane toward the plate. The stapedial muscle converges into a thread-like tendon, which inserts into the middle of the posterior margin of the columella. There is no arteria stapedia present. A pinpoint-size indentation is visible in the columella near its base and is probably an indication for a foramen. The stapes ratio is about 1.4.

Solenodon paradoxus
Figure 4

The tympanic forms an incomplete ring with the incisura open dorsally. It has a small recessus meatus which widens slightly antero-inferiorly. Its posterior crus is in contact with the tympanic process of the periotic. The ventral side of the cavum tympani is not covered by bone.

The malleus and incus have a generalized structure; the articulation is saddle-shaped; the capitular crest is very distinct and the long neck is sharply bent. The large lamina is quadrangular in shape. The distal end of the neck has a well-developed apophysis orbicularis.

The antero-dorsal and postero-ventral faces of the manubrium are flat and it ends in a slender spatula. The posterior (short crus) is short and reaches into the epitympanic recess. The ossicular functional axis angle with the horizontal is about 32° and the lever ratio is 1.2.

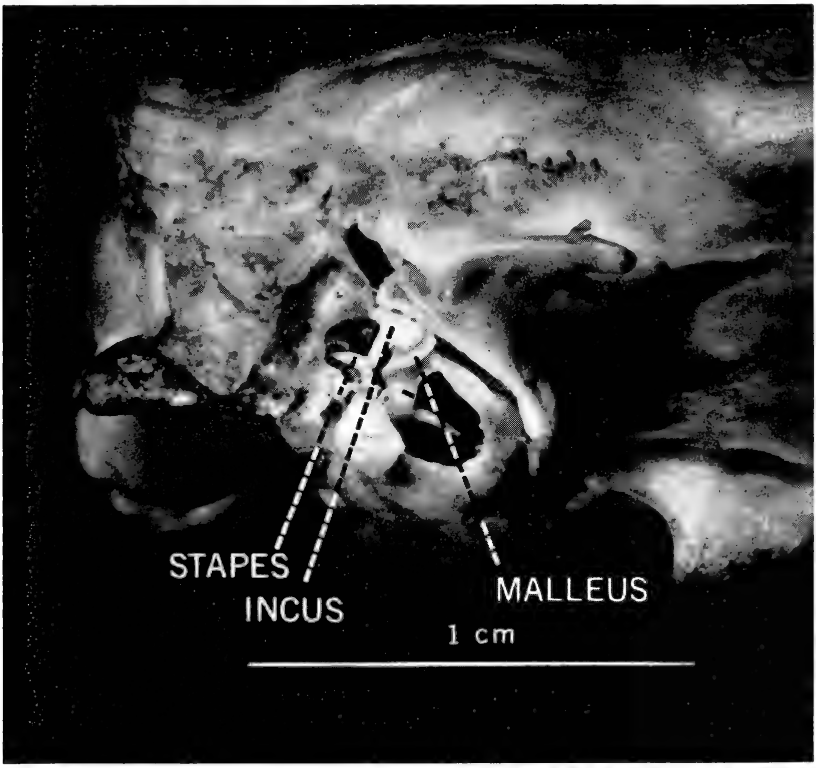


FIG. 5. *Setifer setosus.* Latero-ventral view of right middle ear. (Obscuring bone removed.)

The stapes has a shallow head; the crura are well curved; the posterior less than the anterior. The desiccated stapedial artery occupies the anterior half of the space between them and is not in a bony enclosure. The plate is elliptical, its longitudinal axis forms an angle of about 28° with the horizontal, and the stapes ratio is about 2.0.

Nesophontes edithae

In *Nesophontes* the long stapedial axis forms with the horizontal an angle of about 30° and the stapes ratio is about 2.3.

Setifer setosus

Figure 5

The tympanic is much inclined toward the horizontal and its short recessus meatus is only slightly ascending. The wide incisura tympanica is open dorso-caudally and is covered by the squamosal. The stylohyoid lies on the lateral side of the posterior crus. The anterior crus is covered anteriorly by the tympanic process of the squamosal, further ventrally by the tympanic process of the alisphenoid. The bulla is formed to the greatest extent by the tympanic process of the basisphenoid, which covers the ventral border of the tympanic. Postero-medially, it is in sutural contact with the periotic. Anteriorly, between the tympanic ring, the ali- and basisphenoid, there is an approximately rectangular-shaped opening for the Eustachian tube. The well-developed mastoid points with its distal end in a latero- and slightly ventral direction. It is formed to a great extent by the squamosal, the rest by the periotic.

The malleus has a generalized appearance and is very similar to that of *Solenodon*. The articulation with the incus is saddle-shaped; the capitular crest sharply delineated; the long neck has a prominent hump and an apophysis orbicularis. The lamina is quadrangular.

The posterior crus incudis reaches into the epitympanic recess.

The space between the crura stapedis is wide and the stapedial artery is not enclosed in a bony canal. The ossicular functional axis angle with the horizontal is about 35°, the lever ratio about 1.2, and the stapedial ratio about 2.0.

Echinops telfairi

Figure 6

A large tympanic process of the basisphenoid forms the ventral wall of the cavum tympani and covers the tympanic from below. Posteriorly and postero-medially, it borders on the periotic. The horseshoe-shaped tympanic has a small recessus meatus and a wide incisura tympanica which opens dorso-caudally. Its posterior crus is covered laterally to a great extent by the stylohyoid. The well-developed mastoid process is flattened on its antero-lateral and ventro-medial sides and points latero-ventrally. Its larger anterior part is supplied by the squamosal, the posterior part by the periotic.

The malleus head bears a saddle-shaped articulation and its lamina is quadrangular. The angle in the neck is about 90°. The apophysis orbicularis is well developed and the narrow manubrium ends in a slender spatula.

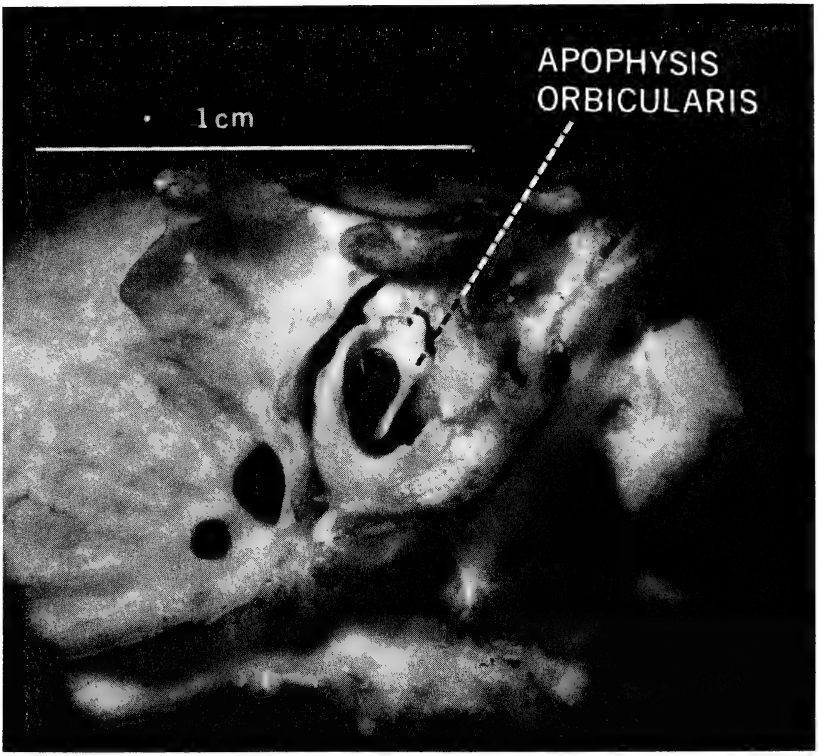


FIG. 6. *Echinops telfari*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

The incus has a robust body. Its stapedial crus is plump and does not diminish in size distally. The short crus is well developed and reaches into the epitympanic recess.

The shallow head of the stapes is oval and the crura are well arched. The angle of the ossicular functional axis with the horizontal is about 36° as in *Tenrec*. The lever ratio is 1.2 to 1.3. The stapes ratio is about 2.0. The stapedial artery is not enclosed in a bony canal and fills only a small part of the intracrural space.

Oryzorictes niger

Figure 7

The horseshoe-shaped tympanic has a very small recessus meatus and is very little inclined from the horizontal. The small incisura tympanica is located laterally and caudo-dorsally and is filled by the

malleus. The cavum tympani is covered below by the tympanic process of the basisphenoid; the latter is in close contact and overlaps part of the tympanic ring. Posteriorly, the tympanic process of the basisphenoid is in sutural contact with the tympanic process of the periotic. The opening for the Eustachian tube is formed by the alisphenoid, the basisphenoid, and the tympanic; the opening for the carotid artery by the tympanic and periotic.

The malleus has a generalized appearance with a sharp capitular crest, a long, sharp-angled neck, a well-formed apophysis orbicularis, and a large quadrangular lamina. The posterior end of the short crus incudis reaches into the epitympanic recess. The ossicular functional axis forms an angle of about 42° with the horizontal plane and the stapes ratio is about 2.2.

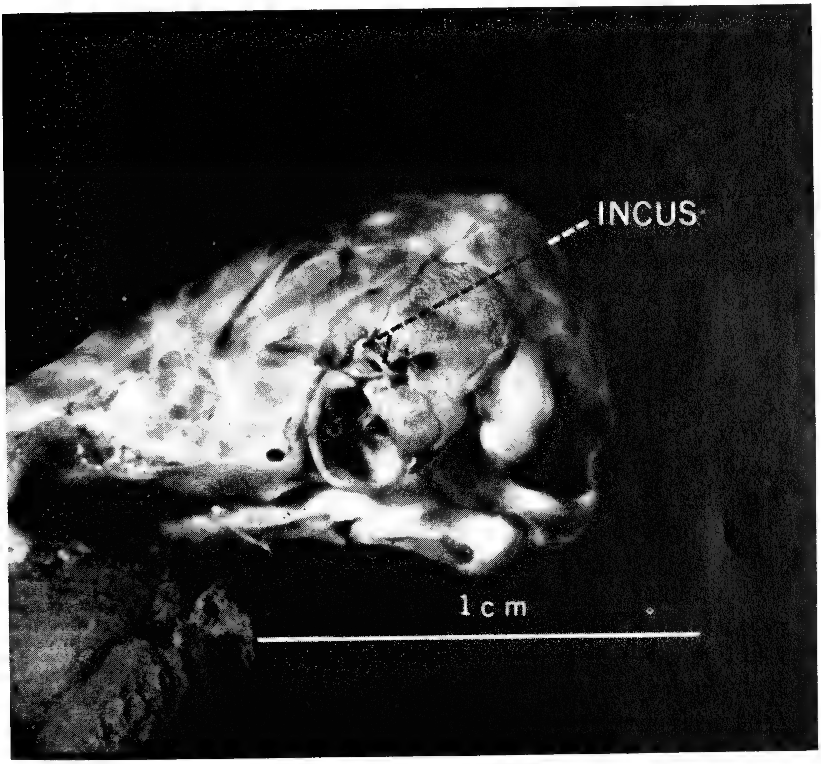


FIG. 7. *Oryzorictes niger.* Latero-ventral view of left middle ear. (Obscuring bone removed.)

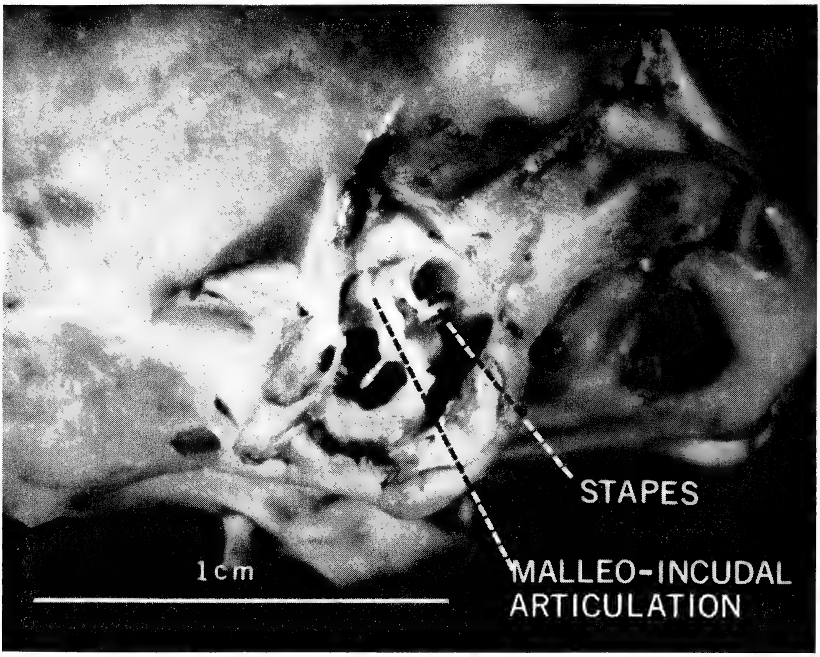


FIG. 8. *Potamogale velox*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

Potamogale velox

Figure 8

A large tympanic process of the basisphenoid covers the cavum tympani ventrally. It reaches laterally beyond the ventral edge of the ectotympanic and is not in close contact with it. The posterior crus of the tympanic is obscured from the lateral view by a post-tympanic process of the squama and further down the stylohyoid, which in turn with its ventral margin is closely attached to the tympanic process of the basisphenoid. Dorso-laterally, the stylohyoid is in contact with the tympanohyale. The opening for the carotid artery is formed by the periotic and by the tympanic process of the basisphenoid.

The neck of the malleus has a hump and a well-developed apophysis orbicularis. Its lamina is relatively small. The manubrium, shaped as in *Echinops*, is directed antero-ventrad and much mediad. The angle of the ossicular functional axis with the horizontal plane is about 40° and the stapes ratio is about 1.9.

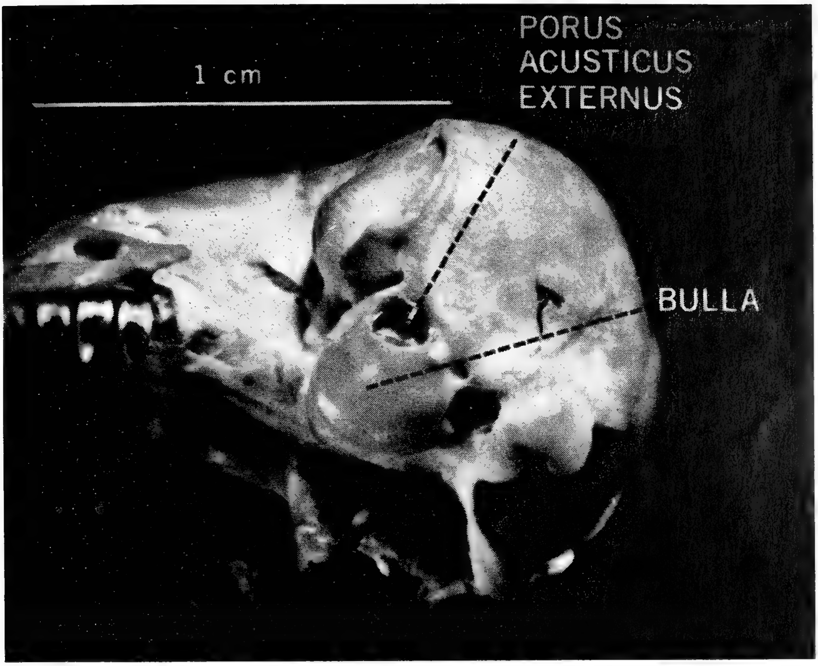
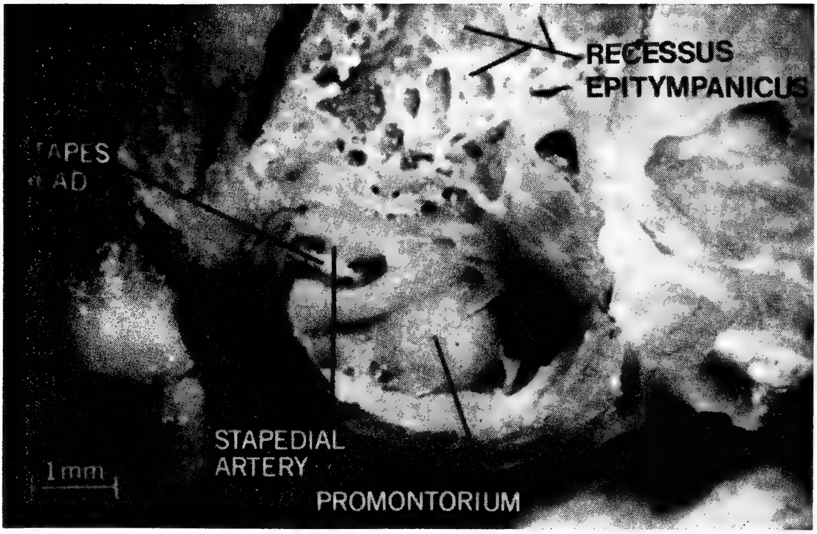


FIG. 9. *Chrysochloris* (*stuhlmanni*?). Latero-ventral view of left auditory region.

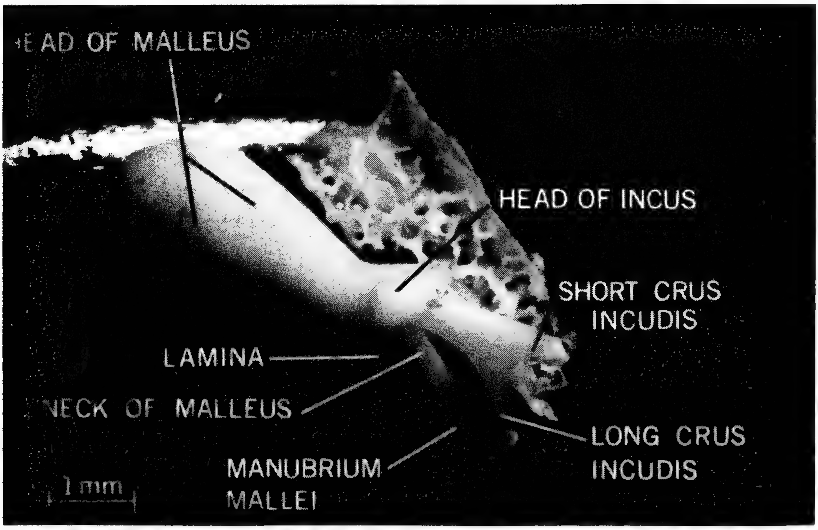
Chrysochloris stuhlmanni
Figures 9, 10A and B

The tympanic forms a long recessus meatus which supplies a large part of the bulla. The porus externus is small and nearly round. Medial and in sutural contact with the tympanic is a tympanic process of the basisphenoid. Posteriorly, this process, the periotic, and the tympanic participate in the formation of the foramen caroticum. The configuration of the external ear of the *Chrysochloris* shows a great similarity to that of *Talpa* and *Notoryctes*. This apparently is due to adaptation to their common environment.

The unusual shape and position of the malleus and incus attracted the interest of many zoologists and I refer to the description by Doran (1877, p. 37). Doran did not find a lamina and speculated on its presence. The specimen studied shows a well-developed, thin, triangular lamina (fig. 10B). The ossicles deviate in their morphology greatly from those of all other insectivores. The stapes, however, has kept its insectivoral character with its well-curved crura between



A



B

FIG. 10. *Chrysochloris* (*stuhlmanni*?). A. Latero-ventral view of right middle ear. (Obscuring bone, malleus, incus removed.) B. Medio-caudal view of right malleus and incus.

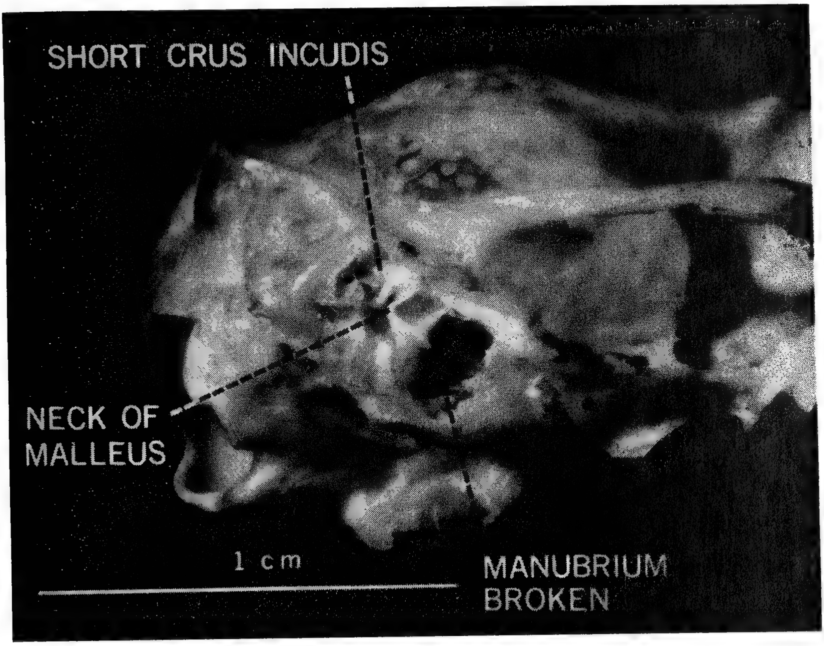


FIG. 11. *Hylomis peguensis.* Latero-ventral view of right middle ear.

which the stapedial artery passes, enclosed in a bony canal, as in Talpidae. The stapedial ratio is about 2.0.

Hylomys peguensis

Figure 11

The tympanic is horseshoe-shaped with a small, only slightly ascending, recessus meatus. The eardrum is very much inclined toward the horizontal. The dorsal end of the anterior crus is bent dorsocaudad. At the bend of the crus originates a short horn-like process which points antero-ventrad. The large tympanic process of the basisphenoid reaches slightly lateral of the ventral edge of the tympanic. Caudally, it is in sutural contact with the tympanic process of the periotic. The foramen caroticum is bordered by the tympanic process of the basisphenoid, the tympanic process of the periotic, and the ectotympanic. The opening for the Eustachian tube is bordered by the tympanic, the tympanic process of the basisphenoid, and the alisphenoid.

The malleus has a saddle-shaped articulation. The neck forms an angle of about 90°, its wide lamina is quadrangular and the apoph-

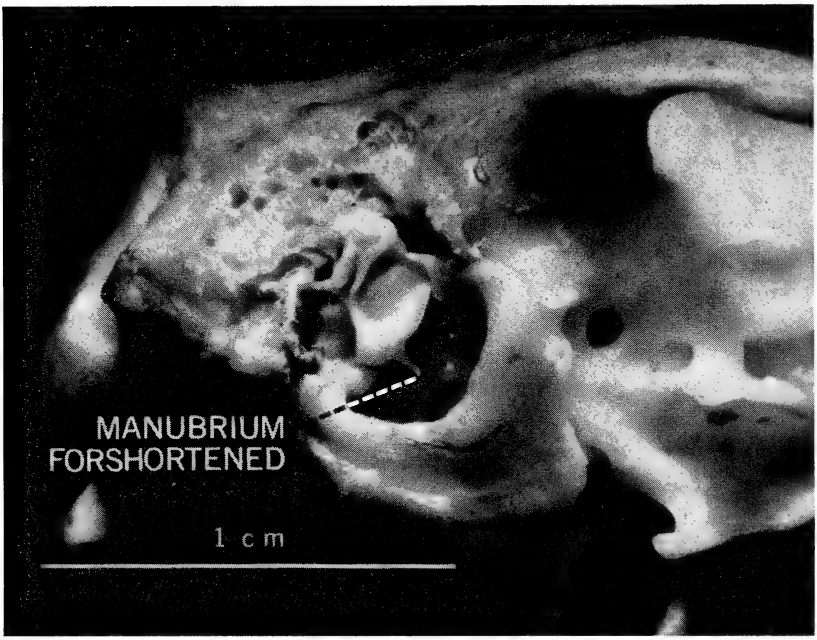


FIG. 12. *Erinaceus europaeus.* Latero-ventral view of right middle ear. (Obscuring bone removed.)

ysis orbicularis is well developed. The short manubrium is flat on its antero-dorsal and postero-ventral side and its distal end is spatulated.

The incus is robust. Its posterior crus reaches into the epitympanic recess and the ossicular functional axis forms an angle of about 27° with the horizontal. The processus lenticularis of the stapedial crus incudis articulates with the shallow caput stapedis.

The stapedial crura are very curved and the elliptical stapes plate has a ratio of 1.9. The stapedial artery passes between the crura in a broad, open, bony trough. The lever ratio is about 1.0.

Erinaceus europaeus

Figure 12

The ectotympanic which has a long recessus meatus is inclined very little from the horizontal. The tympanic cavity is covered ventro-medially by a large tympanic process of the basisphenoid which reaches laterally slightly beyond the ventral edge of the tympanic. Anteriorly, together with the ectotympanic and the alisphenoid, it surrounds an irregularly-shaped opening for the Eustachian tube.

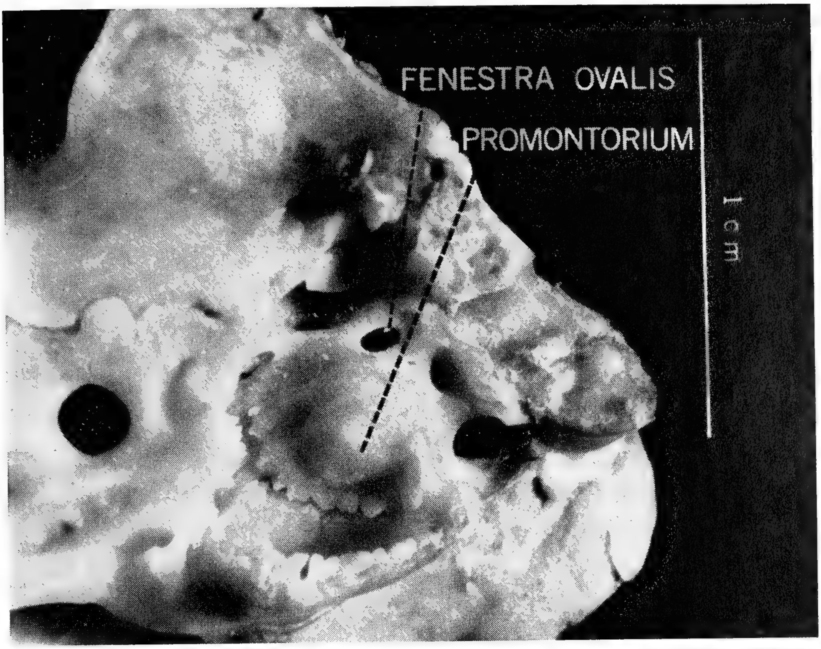


FIG. 13. *Erinaceus europaeus.* Latero-ventral view of left periotic.

Posteriorly, it is in sutural contact with the periotic. In some specimens a stylohyoid obscures the lateral view of the posterior crus of the ectotympanic. The dorsal end of the posterior crus is in contact with the tympanohyale. The large opening for the carotid artery is formed by the tympanic and the periotic. The mastoid process, formed by the periotic, points ventro-laterally.

The malleus has a saddle-shaped articulation. Its long neck is only slightly curved. The lamina is quadrangular and the apophysis orbicularis is only indicated. The manubrium which is severely bent medially, but only slightly antero-ventrally is foreshortened in the figure. The short crus incudis reaches into a fossa incudis in the posterior wall of the cavum tympani. The ossicular functional axis angle with the horizontal is about 20°. The stapedial crus incudis is stout and equal in size along its whole length. The crura are well curved and the artery is not enclosed in a bony canal. The plate is elliptical and the stapedial ratio is about 2.0 (fig. 13).

Hemiechinus auritus

The auditory region is so similar to that of Erinaceus that a separate morphological description seems to be unnecessary. The or-

bicular functional axis angle with the horizontal is about 20° and the stapedial ratio is also about 2.0.

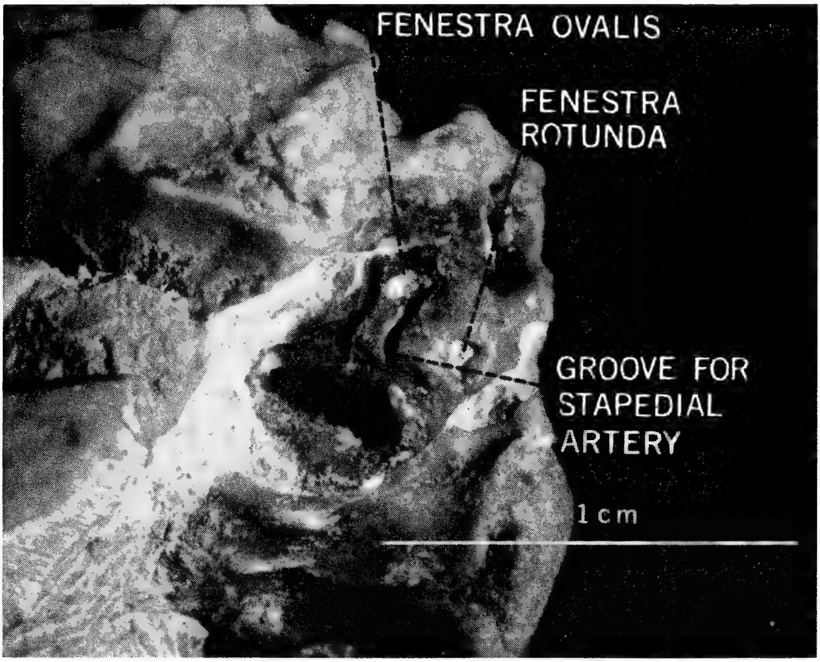


FIG. 14. *Ictops dakotensis*. Latero-ventral view of left periotic.

Ictops dakotensis

Figure 14

A specimen of *Ictops* is available to me in which the periotic with the fenestra ovalis is preserved. The stapedial ratio is 2.0, exactly as in *Erinaceus* (fig. 13).

Elephantulus renatus

Figure 15

The tympanic forms a recessus meatus and a cylindrical ear canal which is directed latero-caudad. The membrana tympani approaches the vertical plane. Medially to the ectotympanic and clearly demarcated from it on the base of the skull is a large entotympanic (Van Kampen, 1905), which contributes the medial and largest part of the bulla. The alisphenoid process together with the squamosal forms the anterior wall of the bulla. The Macroscelidae differ from most

of the insectivores in that the basisphenoid does not participate in the bulla formation. Postero-medially, the entotympanic borders

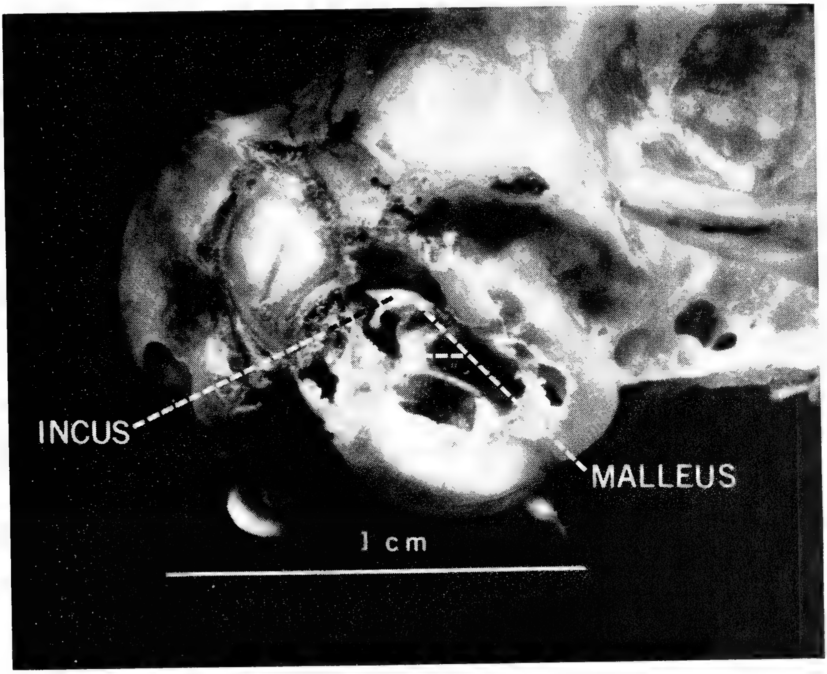


FIG. 15. *Elephantulus renatus.* Latero-ventral view of right middle ear. (Obscuring bone removed.)

the periotic, which participates also in the formation of the bulla. Posteriorly, the entotympanic and the periotic border the foramen caroticum.

The articulation of the malleus is saddle-shaped. Its neck is long and moderately curved. The apophysis orbicularis is well defined; the lamina relatively small; and the manubrium is directed antero-mediad and only slightly ventrad. The angle of the orbicular functional axis with the horizontal measures about 20°. In *Nasilio* this angle is also 20°. The distal end of the short crus incudis lies in a fossa in the posterior wall of the cavum tympani.

The stapes has little curved crura. The stapedial artery lies in an open bony trough. The anterior part of the stapedial plate is wider than the posterior and the stapedial ratio is about 2.0.

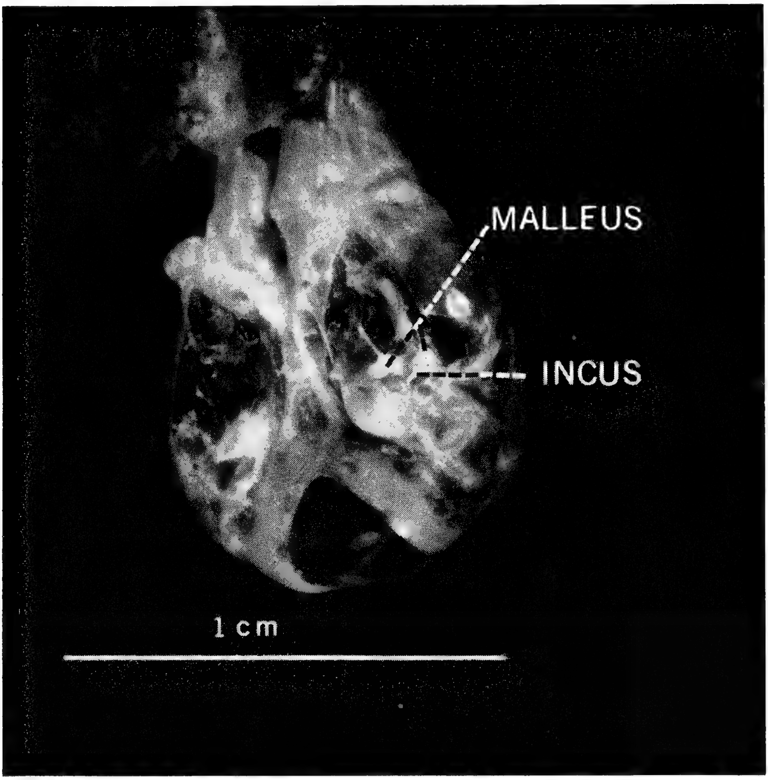


FIG. 16. *Sorex veraespacis.* Latero-ventral view of left middle ear. (Obscuring bone removed.)

Sorex veraespacis

Figure 16

The middle ear is located on the base of the skull. The tympanic forms a nearly complete ring. The minute incisura tympanica is open latero-caudally due to the unusual position of the middle ear. The tympanic is not covered from below and its widest part is antero-medially. Medially, the middle ear is open. The tympanic ring with the membrana tympani is in a nearly horizontal plane and most of the periotic is located caudally from them.

The malleus and incus are of the generalized type. The articulation is saddle-shaped. The long neck has a bend of about 90°. The large, thin lamina is quadrangular and the apophysis orbicularis is large. The thin manubrium is straight and the spatula at the distal end is very slender.

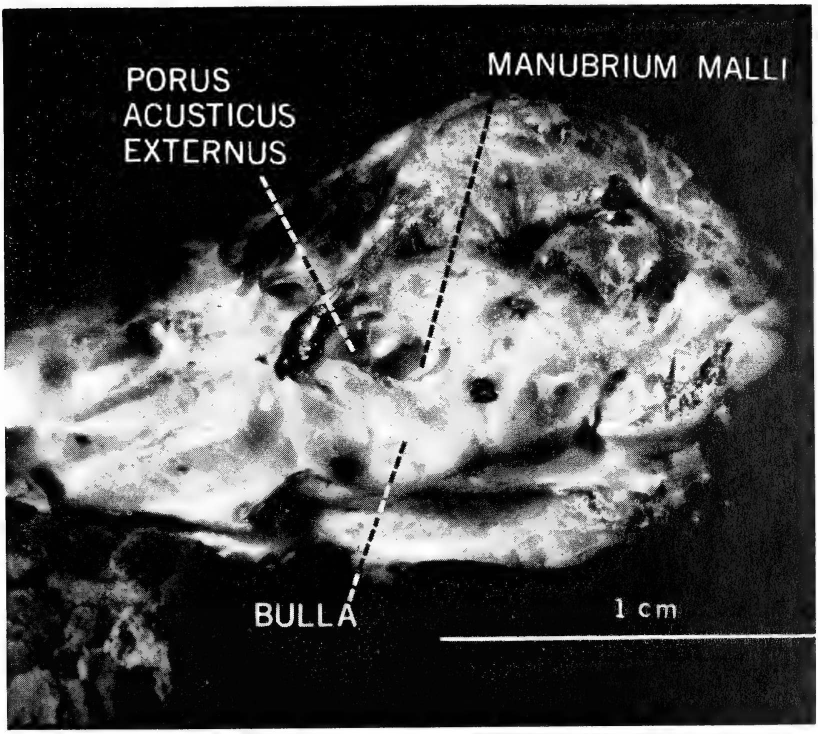


FIG. 17. *Talpa europaea.* Latero-ventral view of right auditory region.

The posterior crus incudis is very short and blunt. The stapedial crura are well curved and the stapedial ratio is about 2.0. The artery is not enclosed in a bony canal.

Blarina and *Crocidura* (stapedial ratio is 2.0) are very similar to *Sorex* and will not, therefore, be separately discussed.

Talpa europaea

Figure 17

The tympanic forms a long recessus meatus, which ascends only slightly laterally. The membrana tympani is only little inclined from the horizontal. Medial to the tympanic is a tympanic process of the basisphenoid, which borders posteriorly on the basioccipital, postero-laterally on the tympanic process of the periotic. The oval-shaped porus acusticus externus is small.

The articulation of the malleus is much flatter than in most other insectivore families (fig. 18). The lamina is triangular and laterally

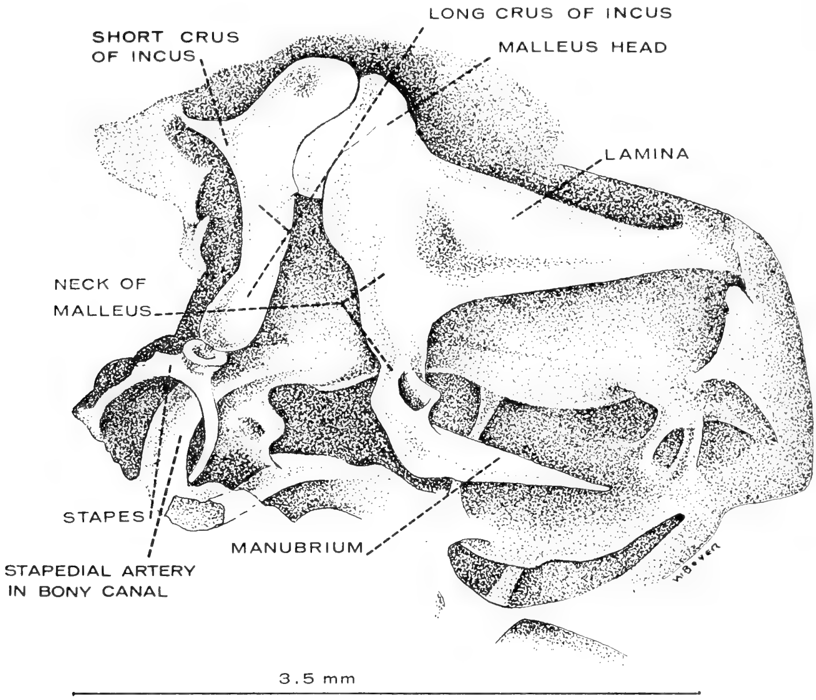


FIG. 18. *Talpa europaea.* Latero-ventral view of right middle ear. (Obscuring bone removed.)

convex. The straight neck is directed ventrad and slightly anteriorly and has no apophysis orbicularis. There is a short, curved, horn-like processus brevis mallei. The manubrium points antero-mediad.

The short crus incudis is finger-like and the stapedial crus is plump and has a cavity antero-medially. The ossicular functional axis is about parallel to the horizontal (+2°) and the lever ratio is about 1.3 to 1.5.

The stapes has a shallow elliptical head. The crura are very curved and between them runs the stapedial artery enclosed in a bony canal. In *Talpa* it fills almost half of the distance between the crura; in *Scapanus,* nearly the whole distance. The stapedial ratio in *Talpa* is about 1.8.

The auditory region of *Scapanus townsendi* and *Scalopus aquaticus* are very similar to *Talpa* and, therefore, will not be described separately.

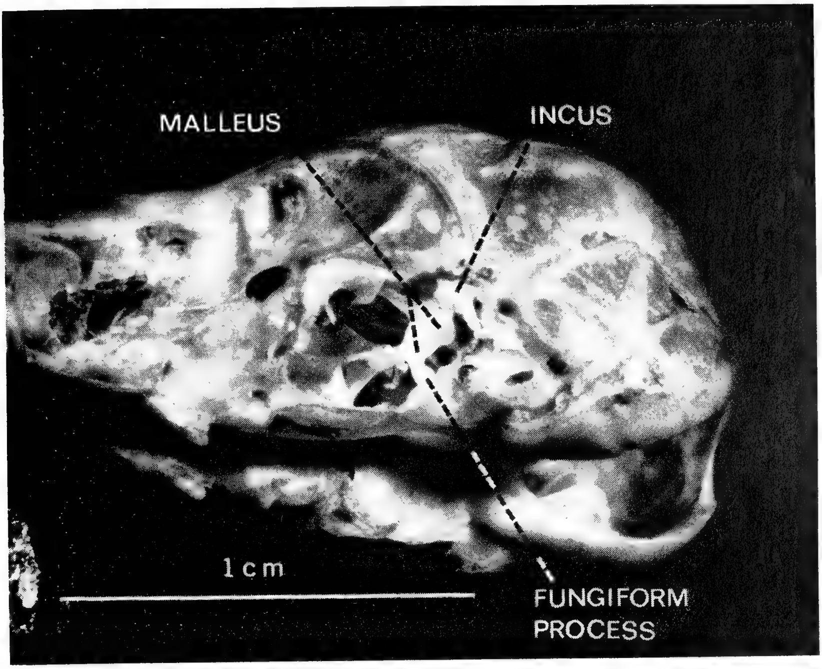


FIG. 19. *Condylura cristata*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

Condylura cristata
Figure 19

The ectotympanic forms a recessus which is much shorter than in *Talpa*. The upper end of the anterior crus is bent sharply caudad and lies against the superficies meatus. The incisura tympanica is open dorso-caudally. The membrana tympani is a little inclined from the horizontal. The ventral wall of the cavum tympani is formed by the tympanic process of the basisphenoid. The postero-medial edge of the latter borders the basioccipital; on its posterior edge, the exoccipital; on its postero-lateral, the tympanic process of the periotic; and on its lateral edge, the ectotympanic. Anteriorly, the basisphenoid forms together with the tympanic and the tympanic process of the alisphenoid a small opening for the Eustachian tube. The opening for the carotid artery is formed by the periotic and ectotympanic.

The articulation of the malleus is saddle-shaped and the two facets form a caudally open angle of about 150°. It differs in that

respect from that of Talpinae and Scalopinae, presumably due to a different function in fossorial mammals. The tympanic plate lies in the horizontal plane and the lamina is about rectangular; triangular in *Talpa*. The neck has, in contrast to *Talpa*, a sharp-angled hump and from its distal end originates a fungiform (puffball) shaped process. Van Kampen (1905) looked upon it as an apophysis orbicularis, which served also for the insertion of the tensor tympani muscle. The bayonet-shaped manubrium points anteriorly.

The short process of the incus is better developed than in *Talpa*. The ossicular functional axis angle with the horizontal is about zero and the lever ratio is about 1.1.

The stapedial artery nearly fills the space between the crura and, as in *Talpa*, is enclosed in a bony canal. The stapedial ratio is about 2.2.

Uropsilus soricipes
Figure 20

The middle ear is located on the base of the skull similar to that in shrews. The tympanic has a well-developed recessus meatus and the membrana tympani are lying nearly in the horizontal plane. Due to the unusual position of the middle ear, the incisura tympanica opens caudo-laterally. The porus acusticus externus is wide. A tympanic process of the basisphenoid covers the lower part of the cleft on the medial side of the cavum tympani between the tympanic resp. membrana tympani and the dorsal wall of the cavum tympani. This process is not present in *Sorex*. The greatest part of the periotic is caudal to the middle ear, as in *Sorex*. Antero-medially, between the ali-, basisphenoid, and the tympanic, is the opening for the Eustachian tube.

The articulation of the malleus is saddle-shaped; the long neck has a marked hump. The thin lamina is quadrangular and the apophysis orbicularis is well developed. The manubrium points antero-ventrad and much mediad. The posterior crus incudis is short and the stapedial crus diminishes distally in size. The angle of the ossicular functional axis with the horizontal amounts to about 5°. The stapedial ratio is about 2.0. The stapedial artery runs in an open trough.

Tupaia palawanensis
Figure 21

The bulla is formed to the greatest extent by a large entotympanic. Its longest axis runs from caudo-lateral to antero-medial.

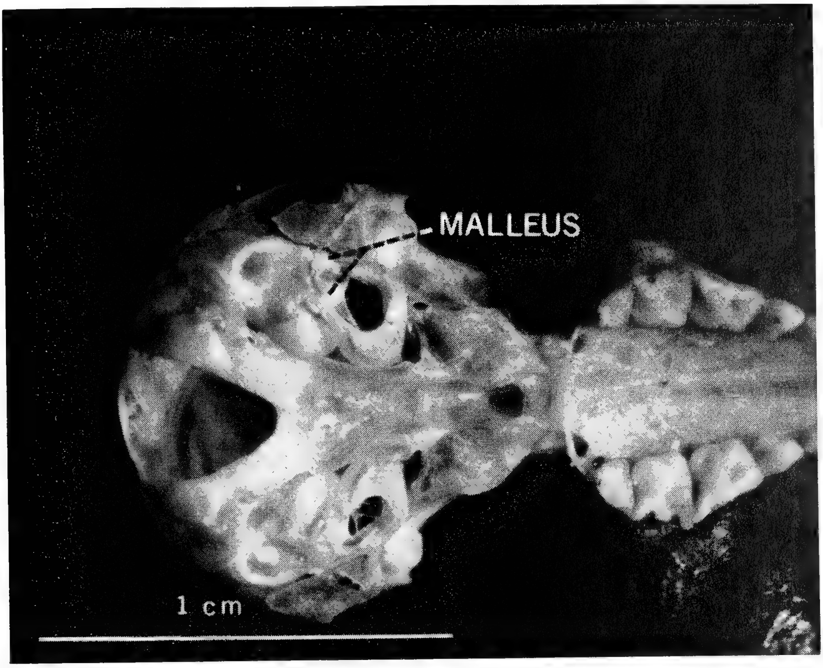


FIG. 20. *Uropsiles soricipes.* Latero-ventral view of left middle ear. (Obscuring bone removed.)

Medially, it borders the basisphenoid and the basioccipital and postero-laterally, the mastoid. Neither the basisphenoid nor the alisphenoid participate in the formation of the bulla. The entotympanic forms a recessus meatus and a short cylindrical ear canal. The small horseshoe-shaped tympanic is only loosely attached to the inside of the entotympanic, which obscures the tympanic from the lateral view to a great extent.

The head of the malleus and the incus reach into the recessus epitympanicus. The anteriorly-pointed head of the malleus has a saddle-shaped articulation and is sharply bent medially, forming with the manubrium an angle of about 115°. The anterior process is short, its lamina is very small. The processus brevis mallei is prominent due to the sharp angle of the head with the manubrium. The latter has a blunt lateral edge and is directed ventrally and very slightly anteriorly.

The body of the incus is robust, its posterior crus very well developed, being nearly as long as or even longer than the stapedial crus.

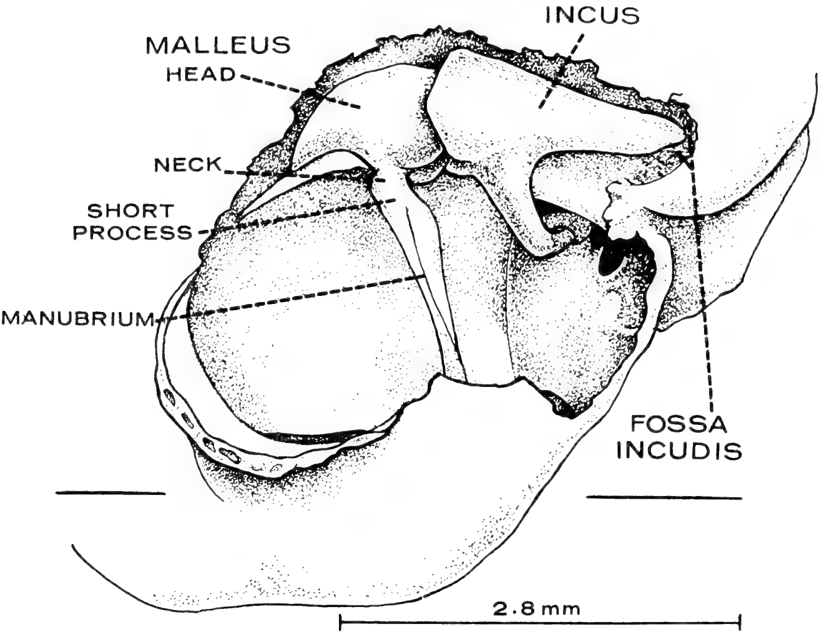


FIG. 21. *Tupaia palawanensis.* Lateral view of left middle ear. (Obscuring bone removed.)

It reaches into the fossa incudis in the posterior wall of the cavum tympani.

The stapedial crura are only slightly curved and form an oval foramen which is nearly filled by the large stapedial artery. The latter is enclosed in a bony canal, which is interrupted between the crura.

The foramen for the carotid artery is formed postero-medially by the periotic, which comes in the form of a short, small strip to the ventral surface of the skull. The rest of the circumference is supplied by the entotympanic.

The angle of the ossicular functional axis with the horizontal is about +5°. The very elongated stapedial plate has a ratio of about 2.9, which is greater than that in any other insectivore examined.

DISCUSSION

Ectotympanic, Entotympanic, and Tympanic Process of the Basisphenoid

The auditory region undergoes specialization which becomes manifested in various degrees of participation of the ectotympanic

(tympanic), the tympanic process of the basisphenoid, and the entotympanic in the formation of the bulla and in the degree of complexity to the organization of these elements.

There is no recessus meatus in the primitive auditory regions of *Sorex* and hardly any in *Solenodon*. In all other genera a recessus meatus is present. With progressive specialization of the auditory region the recessus increases in size.

A tympanic process of the basisphenoid is not present in *Sorex* and *Solenodon*. *Didelphis*, among the marsupials, corresponds to some extent with this degree of differentiation. There is, however, already a partial cover (alisphenoid) anteriorly on the ventral side of the cavum tympani. All other insectivore genera have a tympanic process of the basisphenoid with the exception of *Macroscelides* and *Tupaia*, where it is supplanted by an entotympanic. The tympanic process extends in most genera from the midline to lateral of the ventral edge of the ectotympanic. In the generalized genera, as in *Potamogale*, it has no contact with the ectotympanic on the macerated skull. In the specialized genera, as in *Erinaceus*, it turns around the ventral edge to the lateral side of the ectotympanic and the two structures can easily be separated. In the Talpidae and Chrysochloridae the tympanic process of the basisphenoid is in sutural contact with the ectotympanic.

The presence of an entotympanic is not characteristic for either order. It is found in several families of marsupials, as well as insectivores, and increases in size with progressive specialization of the auditory region. There is none in *Sorex* and *Solenodon*; a large one in *Macroscelides*; and the largest in *Tupaia*. Similarly, among the marsupials, *Didelphis* has a very small entotympanic and *Dromiciops* a large one.

Ossicles

Like the structures discussed above, the ossicles also exhibit various degrees of specialization. This applies mostly to the malleus, less to the incus, and relatively little to the stapes.

Malleus

The malleus shows greater variation in its morphology than the incus. This agrees with my observation in the marsupials. In the latter it was possible to show the interrelationship between the tympanic and the malleus and explain them with their common ontogeny

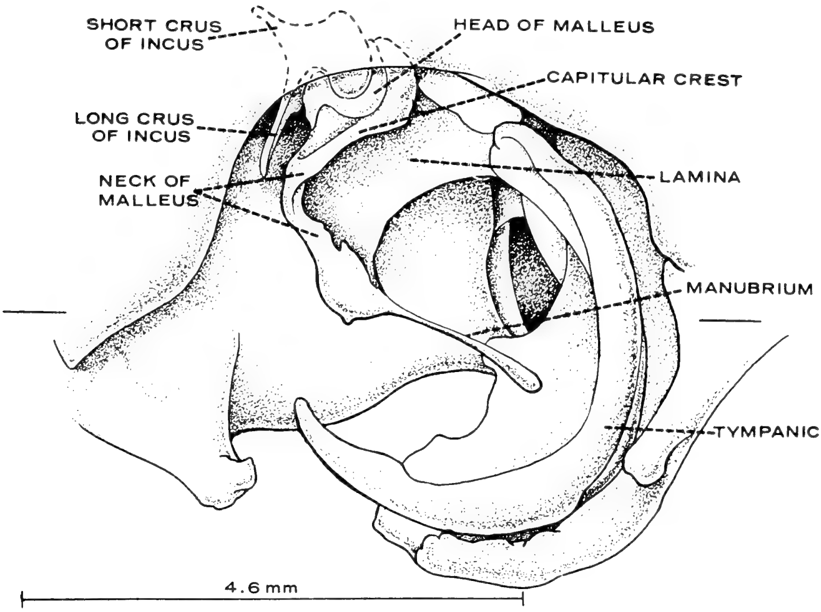


FIG. 22. *Didelphis albiventris.* Lateral view of right middle ear.

and their close mechanical relationship. The changes in the tympanic are probably primary due to its greater exposure to outside mechanical forces; those of the malleus secondary (Segall, 1969 b). A similar situation prevails in the insectivores. The malleus has a generalized form in the majority of the genera. The articulation is saddle-shaped, except in the Talpidae, Scalopinae, and Chrysochloridae, where it is much flatter.

The neck of the malleus is long and shows a sharp bend in the generalized forms. In the more specialized Erinaceidae, the bend is reduced to a slight curve. The Talpidae have a nearly straight neck and in the Tupaiidae, the neck is practically missing.

The lamina is large, thin, and quadrangular in the generalized genera. In the Talpinae it is much smaller, triangular, and laterally convex. In *Condylura* the lamina is somewhat rectangular, different from that in *Talpa.* The malleus of *Tupaia* has a very small lamina only. The reduction in the size of the lamina is approximately paralleled by the reduction in length of the neck.

The apophysis orbicularis is well developed in the generalized forms; becomes sessile, then indistinct in the more specialized genera; and finally disappears altogether. This can be well observed in the

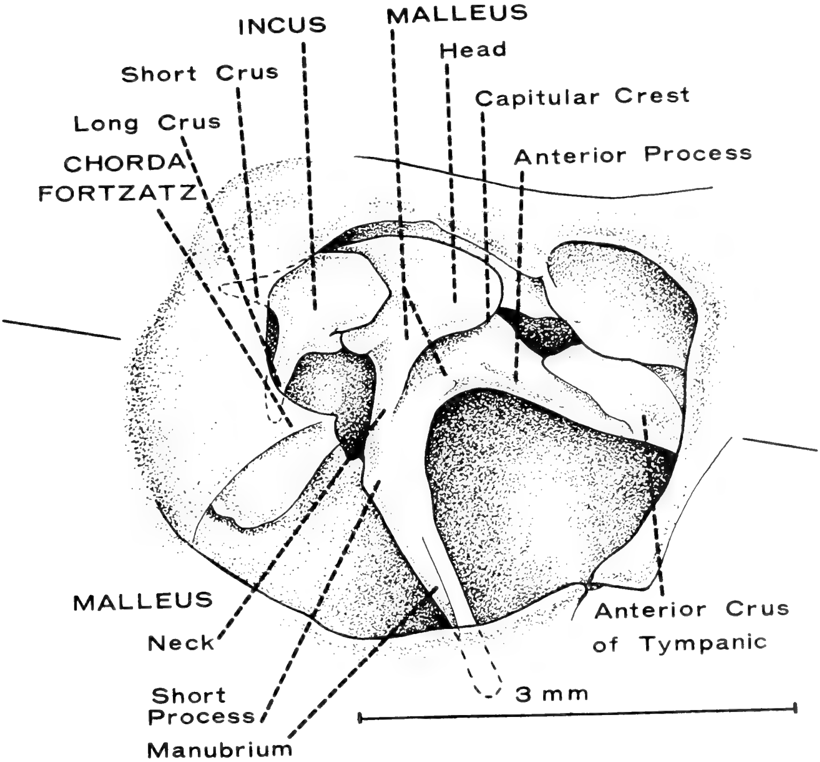


FIG. 23. *Dromiciops australis.* Lateral view of right middle ear.

Erinaceidae, where *Hylomis* and *Echinosorex,* which represent the more generalized genera, have a well-developed apophysis orbicularis while the more specialized *Erinaceus* and *Hemiechinus* have only an indication of it. There is none in the Talpidae. The disappearance of the apophysis orbicularis goes parallel with the straightening of the neck. A similar condition of the lamina and apophysis orbicularis can be seen in the marsupials (Segall, 1969b).

The angle between the neck and manubrium is antero-ventrally and slightly medially directed in some families. In *Erinaceus* and *Hemiechinus* the angle is open antero-ventrally and very much medially. In *Tupaia* the membrana tympani with the manubrium stands in a nearly vertical plane and the head of the malleus is severely bent medially against the latter.

The mallei in both orders with very generalized auditory regions, as in *Solenodon* (fig. 4) and in *Didelphis* (fig. 22), are very sim-

ilar to each other. The same applies to genera with very specialized auditory regions like those in *Tupaia* (fig. 21) and *Dromiciops* (fig. 23.)

Incus

The incus shows, in general, few morphological differences in the various families. The posterior crus is short in the generalized taxa and its posterior end rests in most genera in the epitympanic recess; only in the most specialized ones does it reach into a fossa incudis in the posterior wall of the cavum tympani. The modification of the incus in the fossorial genera is striking. This can be seen in the insectivores (*Talpa,* fig. 18 and *Chrysochloris,* fig. 10b) as well as in marsupials (*Notoryctes,* figs. 3, 3A).

The position of the short crus is a determining factor in the direction of the ossicular functional axis (see *Methods* and *Material*). The angle between the ossicular functional axis and the horizontal plane tends to be greater in the generalized forms. Viewed from the right side, the axis turns with increased specialization counterclockwise and the angle with the horizontal plane becomes successively smaller and even negative (fig. 24). A similar turning of the ossicular functional axis can be observed in the marsupials (Segall, 1969 b).

At a certain stage of rotation of the ossicular functional axis a change in the morphology of the malleus takes place. This is presumably a phyletic response to changing mechanical requirements. In *Hylomys,* where the angle of the axis with the horizontal is already reduced to about 27°, the malleus has still preserved its generalized form. In *Erinaceus* and *Hemiechinus,* however, where the angle is reduced to about 20°, the malleus shows morphological changes. These changes become marked when the angle comes close to the zero point, as in *Talpa.* This is especially true in *Tupaia* in which the differentiation of the malleus is similar to that of the primates. A similar condition occurs in *Dromiciops* among the marsupials (Segall, 1969 a).

The similarity among fossorial genera applies to the external appearance of the auditory region and to the articulation between malleus and incus. Both characters are presumably correlated by a modified function in subterranean environment.

Stapes

The insectivore stapes does not change to any extent with progressive specialization of the auditory region, in contrast to malleus and incus. Even in the highly specialized Talpinae and still more in

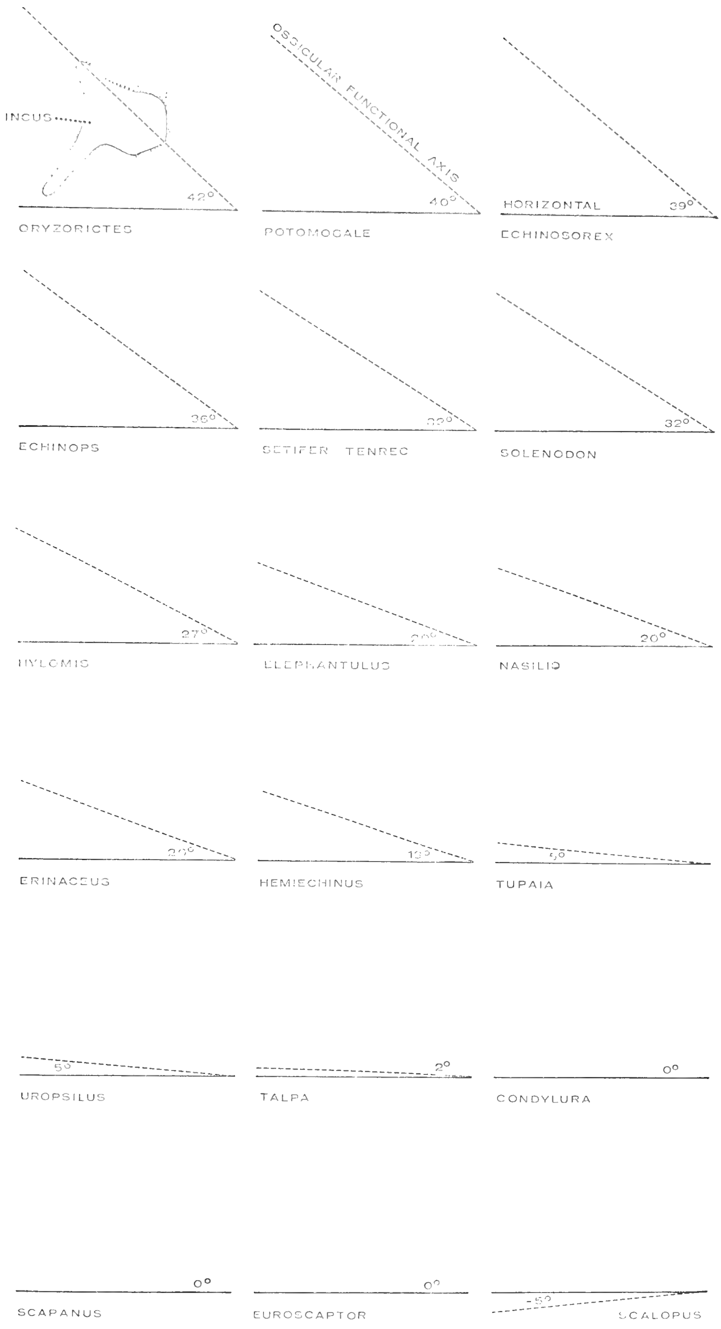


FIG. 24. The angle of the ossicular functional axis with the horizontal plane in insectivores.

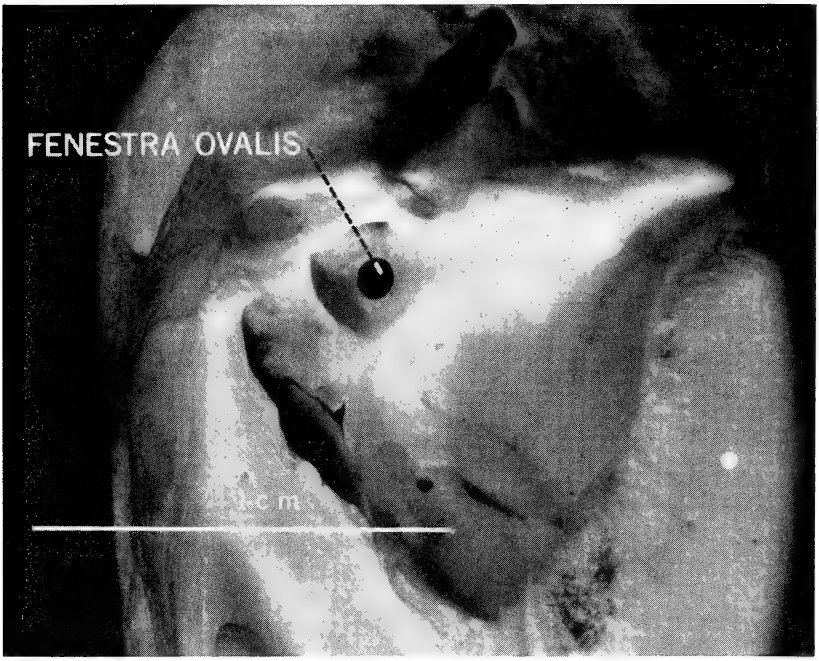


FIG. 25. *Tachyglossa aculcata.* Ventral view of periotic.

the Chrysochloridae, where the malleus and the incus have a unique morphology, the stapes does not differ from that of other insectivores. The near constancy of the stapes ratio of the plate (or the fenestra ovalis) is of taxonomic interest, especially in fossils.

Furthermore, the position of the plate or the fenestra ovalis, with regard to the horizontal plane is of comparative anatomical interest in closely related forms. Both the position and the shape of the stapedial plate can contribute to the identification of fossils. For example, the foramen ovale of the fossil erinaceoid genus *Ictops* (fig. 14) has a stapedial ratio and position identical to those of *Erinaceus* (fig. 26).

A primitive form of mammalian stapes is found in the monotremes. This type of stapes has a columella without opening (stapedial foramen) and a circular plate (stapes ratio 1.0, fig. 25). The marsupials, in which some genera approach the monotremes in this respect while others are much advanced, have stapedial plates with ratios ranging from 1.1 to 2.1. With progressive specialization of the auditory region the stapes ratio increases in marsupials (fig. 26).

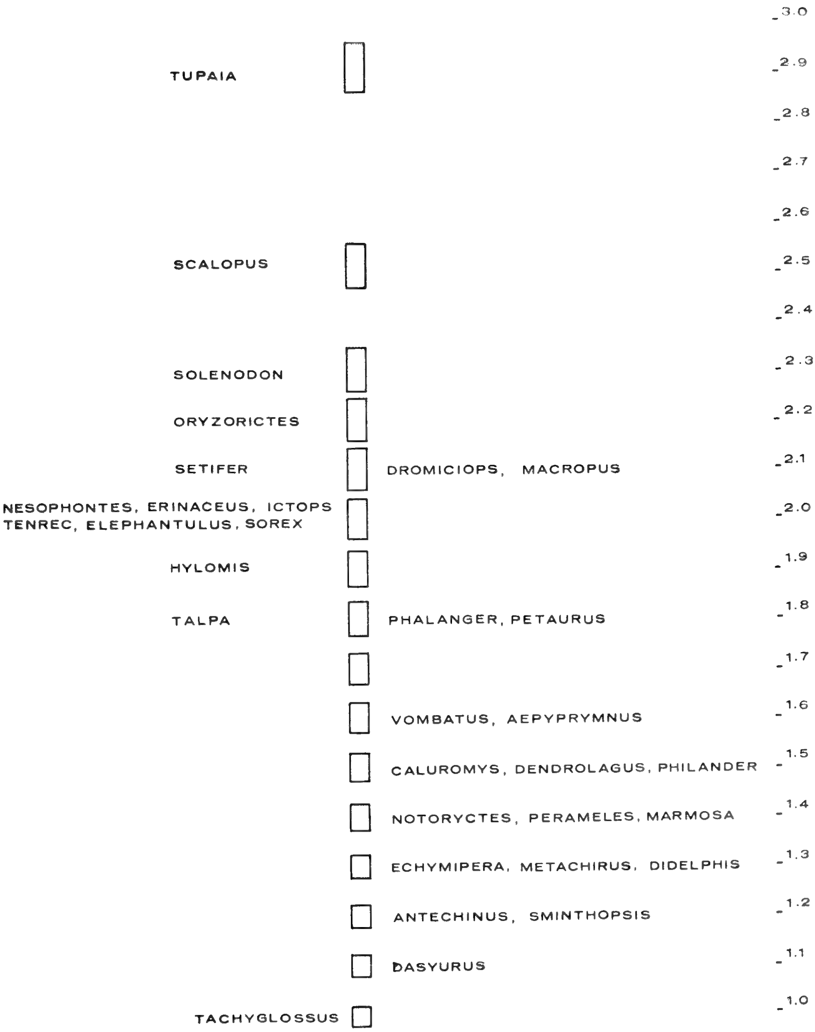


FIG. 26. The stapedial ratio: *a*, in monotremes (below); *b*, in marsupials (right side); *c*, in insectivores (left side).

At the same time, the space between the crura (absent in the columella-like stapes) enlarges only slightly in the marsupials, while the stapes plate may expand considerably. The stapedial foramen in marsupials, if present at all, is always small and never reaches the size commonly observed in insectivores.

In *Notoryctes* the malleus and incus have a morphology that is quite different from that of any other marsupial (fig. 3). The stapes, however, retains its marsupial character. It has a flat columella with a shallow groove at the base, but no canal. Specialization of malleus and incus, but not of the stapes, may be related to the fossorial habit of *Notoryctes*. The same two elements are modified in fossorial insectivores (Talpinae and Chrysochloridae), while the stapes retains its typical insectivore character.

The morphology of the stapedial plate changes first, that of the crura afterward. It is presumably the function that determines the configuration of the plate. The presence, absence, or degree of development of the stapedial artery is not directly correlated with the size of the opening between the crura and it only occasionally fills it completely.

The round shape of the plate and fenestra ovalis is a primitive mammalian character; the elliptical shape, a specialized one.

The present study has shown that the stapes is characteristic in each of the two orders of mammals considered. In the marsupials there is a progressive specialization of the stapes from a columella-like form with a round plate to a stapes with a small opening between the crura and an elliptical plate, while in the insectivores it is invariably stirrup-shaped, irrespective of the general level of specialization of the genus.

In contrast, the ectotympanic, malleus, and incus in both orders show similar, parallel, progressive morphological changes with overall increase of specialization of the genera.

In both orders, furthermore, fossorial genera show marked deviations from the typical condition of malleus and incus, but not of the stapes. It was suggested that these profound changes are related to the fossorial habits.

ACKNOWLEDGEMENTS

I am grateful to Dr. S. Anderson for the loan of a *Notoryctes typhlops* skull and Dr. R. H. Tedford for five *Nesophontes* skulls and for reviewing this paper.

Field Museum placed the entire mammal collection at my disposal. I am especially indebted to Dr. William Turnbull, Dr. R. Zangerl, and Dr. K. Liem for their generous help. In addition, I would like to thank Mr. W. Boyer and Mr. S. Grove for the illustrations and Mr. H. Holden for his great effort with the photographic work. I also thank Miss J. L. Williams for typing the manuscript.

REFERENCES

DORAN, A. H. G.

1877. Morphology of the mammalian ossicula auditus. Trans. Linn. Soc. London, **1**, pp. 371–497.

KAMPEN, P. N. VAN

1905. Tympanalgegend des Säugetierschädels. Morph. Jahrb., **34**, pp. 321–722.

SEGALL, W.

1969a. The middle ear region of *Dromiciops*. Acta anat. **73**, no. 4, pp. 481–501.

1969b. The auditory ossicles (malleus, incus) and their relationship to the tympanic in marsupials. Acta anat. **73**, no. 2, pp. 176–191.

SIMPSON, G. G.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85**, 350 pp.

WEBER, M.

1928. Die Säugetiere. Gustav Fischer, Jena.

THE SYSTEMATICS AND ZOOGEOGRAPHY OF THE AMPHIBIA OF BORNEO

ROBERT F. INGER

FIELDIANA: ZOOLOGY
VOLUME 52
Published by
FIELD MUSEUM OF NATURAL HISTORY
NOVEMBER 23, 1966

FIELDIANA: ZOOLOGY

A Continuation of the

ZOOLOGICAL SERIES

of

FIELD MUSEUM OF NATURAL HISTORY

VOLUME 52

FIELD MUSEUM OF NATURAL HISTORY
CHICAGO, U.S.A.
1966

THE SYSTEMATICS AND ZOOGEOGRAPHY

OF

THE AMPHIBIA OF BORNEO

THE SYSTEMATICS AND ZOOGEOGRAPHY
OF
THE AMPHIBIA OF BORNEO

ROBERT F. INGER

Curator, Reptiles and Amphibians

FIELDIANA: ZOOLOGY

VOLUME 52

Published by

FIELD MUSEUM OF NATURAL HISTORY

NOVEMBER 23, 1966

Edited by EDWARD G. NASH
PATRICIA M. WILLIAMS

Library of Congress Catalog Card Number: 66–28386

PRINTED IN THE UNITED STATES OF AMERICA
BY FIELD MUSEUM PRESS

CONTENTS

CONTENTS

INTRODUCTION

The last systematic review of the frogs of Borneo was published forty years ago and was included as part of a general review of the fauna of the Indo-Australian Archipelago (van Kampen, 1923). Virtually no information on habits and no zoogeographic analysis were given in van Kampen's monograph, which was based mainly on collections made during the 19th century and the first decade of this century. Minor collections were made after that chiefly in Sarawak and Sabah,[1] and formed the basis of three short papers by M. A. Smith (1925A and B, 1931A).

These were the last works on the Bornean fauna *per se*, though generic and family revisions have dealt with some Bornean species (e.g., Barbour, 1938; Parker, 1934). In the meantime some papers were published on the amphibians of other parts of the East Indies. The most important of these (Mertens, 1930, 1934) made significant contributions to our understanding of the distribution of these animals in this area.

Beginning in 1950 the tempo of collecting and observing frogs in Borneo increased. Field Museum of Natural History sent four expeditions to Borneo (1950–1964), the Sarawak Museum renewed its old function of sampling the local fauna but at a much more intensive level, and local naturalists, particularly Neville S. Haile, began to make their efforts felt. The result of all of this activity was the accumulation of many specimens and field notes on habitats and habits. The data made necessary at least a taxonomic review of this rich fauna.

This new material also presented an opportunity to re-evaluate the zoogeography of the amphibians of Borneo. The largest land mass in the part of the East Indies lying in the Oriental Region, Borneo shares much of its fauna with neighboring islands and the adjacent mainland (Darlington, 1957). Analysis of the geographic relations of the Bornean fauna, therefore, subsumes analysis of most of the amphibians of this extensive, rich area.

[1] Formerly known as North Borneo.

Materials and Methods

Four major collections form the basis of this study: those of the British Museum (Natural History), Field Museum of Natural History, Rijksmuseum van Natuurlijke Historie, and Sarawak Museum. Through good fortune, I was able to see all 89 of the Bornean species, 61 of them in life, and to study types of 59 species and 20 synonyms. Most Bornean specimens and many critical specimens from adjacent areas were available to me from the following institutions and collections:

Academy of Natural Sciences, Philadelphia	ANSP
American Museum of Natural History	AMNH
British Museum (Natural History)	BM
California Academy of Science	CAS
Collection of John R. Hendrickson	JRH
Field Museum of Natural History	FMNH
Museo Civico Genova	MCG
Museum of Comparative Zoology	MCZ
Museum National d'Histoire Naturelle, Paris	MHNP
Museum Zoologicum Bogoriense	MZB
Naturhistorisches Museum Wien	NHMW
Naturhistorisches Museum Basel	NMB
Collection of Neville S. Haile	NSH
Rijksmuseum van Natuurlijke Museum	RMNH
Sarawak Museum	SM
Natur-Museum und Forschungs Institut Senckenberg	SNG
Singapore National Museum	SNM
Division of Systematic Biology, Stanford University	SU
University of Michigan Museum of Zoology	UMMZ
United States National Museum	USNM
Zoologisch Museum Amsterdam	ZMA
Zoologisches Museum Berlin	ZMB
Zoologisches Museum Hamburg	ZMH

For adults of most species only three measurements were made: snout-vent length—total length of head and body; head width—taken at temporal region; tibia length—measured on flexed leg from convex surface of knee to convex surface of tibio-tarsal joint. Other measurements are explained where they appear in the text. In describing larvae I have used the stages defined by A. C. Taylor and Kollros (1946).

Synonomies include the original reference, the first use of the present name, all references to Bornean specimens, and all synonyms of Bornean forms.

Following a general statement of the range of each species, I have given a list of all Bornean localities. Literature references are given only for those localities from which I have not seen specimens. The spelling of most place names is taken from the gazetteers of the United States Board on Geographic Names (Gazetteers no. 10 and 13).

Acknowledgments

Primary support for this investigation came from Field Museum of Natural History with important financial assistance for field work and study trips from United States National Science Foundation grants G 6257, G 20867, GB 1049.

Critical aid in the field came from various agencies of the governments of Sabah and Sarawak. In particular I owe my thanks to Mr. and Mrs. Tom Harrisson and Mr. Loh Chee Yin of the Sarawak Museum; Mr. E. J. H. Berwick, Agriculture Department, Sabah; and to Messrs. G. S. Brown, F. V. Webster, and G. Wood, Forestry Department, Sabah. I also received important assistance and hospitality from Messrs. O. C. Finch, J. Hedley, and J. Shelley of Bombay-Burmah Trading Corporation, Ltd., and from Messrs. Lai Fook Kim and Lai Kim Foh of United Timbers, Ltd.

A number of companions in the field made the work not only more profitable, but also more pleasant. In this connection I am especially grateful to Gaun Sureng, Sarawak Museum; Chin Phui Kong, Agriculture Department, Sabah; Neville S. Haile, Geological Survey Department, Sabah; and D. Dwight Davis, Field Museum of Natural History.

Important additions to our collections were made by Messrs. James P. Bacon, William Hosmer, and F. Wayne King. It is a pleasure to acknowledge my gratitude to them.

I also wish to thank the following persons for the privilege of examining specimens under their care: E. Alfred, M. Boeseman, C. M. Bogert, L. D. Brongersma, W. C. Brown, D. M. Cochran, J. Eiselt, L. Forcart, A. G. C. Grandison, J. Guibé, N. Hartweg, D. Hillenius, K. Klemmer, C. Kosswig, A. E. Leviton, A. Loveridge, R. Mertens, G. S. Myers, E. Tortonese, M. F. Tweedie, C. F. Walker, H. Wermuth, E. Williams.

This work has benefited from the advice and criticism of Messrs. H. S. Dybas and H. Marx, Field Museum of Natural History. The drawings are the work of Miss Janet Wright, Mr. John Pfiffner, and Miss Marion Pahl, formerly or now on the staff of Field Museum of Natural History. Mrs. M. Anderson typed the manuscript.

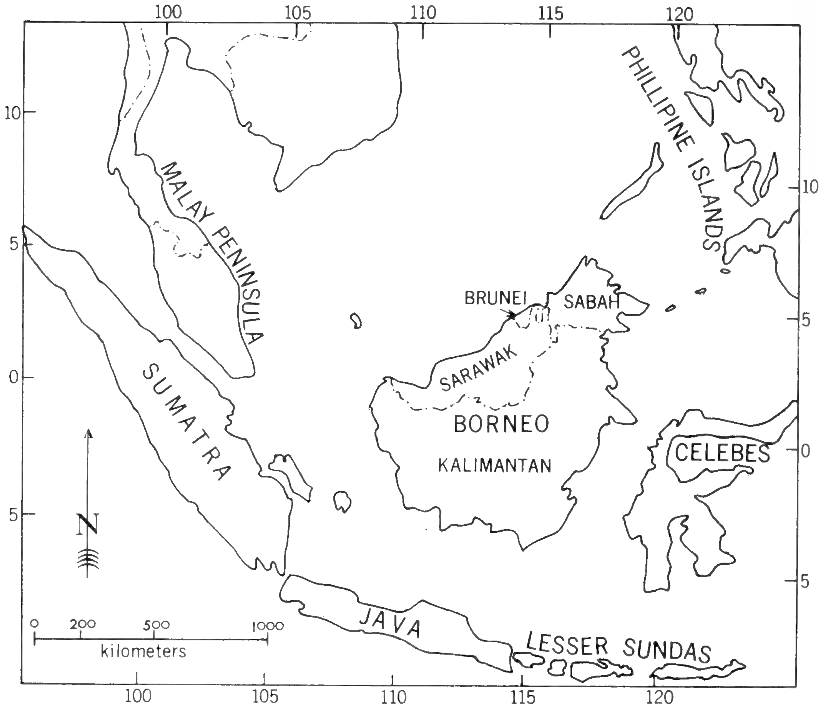


FIG. 1. Map of Borneo and adjacent areas.

ENVIRONMENT

Geography and geology.—Borneo (fig. 1), the third largest island in the world, has an area of 286,969 square miles (Columbia Lippincott Gazetteer of the World), somewhat larger than the state of Texas (263,644 sq. mi.) and still larger than France (212,659 sq. mi.). It extends roughly from 4° S to 7° N and from 109° to 119° E. Four political subdivisions exist: Kalimantan (Indonesia), Brunei, Sabah (Malaysia), and Sarawak (Malaysia).

Borneo lies on the eastern edge of the Sunda Shelf which is part of the continental mass of Asia. The South China Sea, which separates Borneo from the Malaya Peninsula and Sumatra to the west, and the Java Sea south of Borneo are less than 200 meters deep in this area. To the east Borneo is separated from Celebes by the narrow but deep (in excess of 2000 m.) Makassar Straits. Shallow strips of ocean, for the most part less than 200 m. deep, extend north and

northeast from Borneo to the Philippine Islands around the flanks of the deep Sulu Sea.

The center of Borneo consists of an irregular mass of hills and low mountains slightly displaced to the northwest, leaving wider bands of relatively flat lowlands along the east, south, and southwest. Though much of the mountainous area is higher than 1000 m., only small bits of it reach 2000 m. Mount Kina Balu (4100 m.) is the only peak above 3000 m. Extensive swampy areas exist along the coast in central Sarawak and in deeper zones in southern and eastern Kalimantan.

Detailed analysis of the geological structure and history of Borneo is a continuing activity of the Malaysian Geological Survey. The annual reports of this organization and its Bornean antecedent (Geological Survey Dept., British Territories in Borneo) contain much information. A summary of the geologic history of Sabah was published by Reinhard and Wenk (1951). Umbgrove's work (1949) on the East Indies presents the broader outlines that are usually more helpful to a zoogeographer. The following very brief review is based on these works.

Large portions of Borneo are covered by Tertiary deposits with only scattered areas of Mesozoic and older rocks. Igneous rocks of varying ages, from Mesozoic to Quaternary, are widely distributed.

Much of western Borneo has been subaerial through most of the Tertiary and Quaternary. These land areas extended across what is now part of the South China Sea and included eastern Sumatra and the Malay Peninsula (fig. 2). Portions of eastern Borneo were areas of subsidence and deposition in the early Tertiary, but were subjected to folding and erosion from the late Pliocene onward. The significant fact, from the zoological viewpoint, is that much of Borneo and the Sunda Shelf was available for habitation by terrestrial and freshwater animals throughout the Tertiary.

During the Pleistocene, glaciations in the northern hemisphere resulted in lowered sea levels. Kuenen (1950) estimates that sea level was lowered about 90 m. in the area of the East Indies. It is certain that during glacial periods Borneo, Sumatra, Java, and the Malay Peninsula were connected by subaerial land. The courses of drowned river valleys can be detected in the shallow seas that now separate these land masses (fig. 3). Whether the Sunda Shelf was inundated during each interglacial stage of the Pleistocene or was inundated only at the end of the Pleistocene is still uncertain. There is ample evidence of Pleistocene and post-Pleistocene movements in this re-

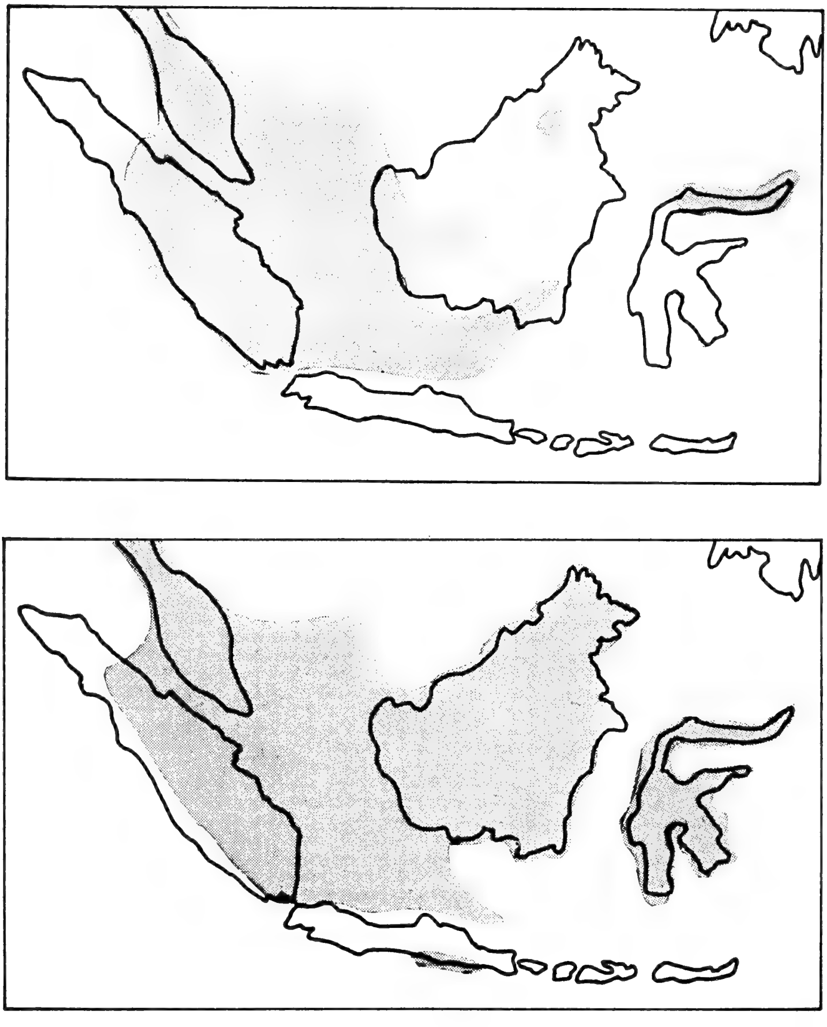


FIG. 2. Probable subaerial land during Eocene (upper) and Pliocene (lower). Adapted from Umbgrove (1949).

gion. The inundation of the Sunda Shelf may have resulted from eustatic rise in sea level following melting of glaciers, or from an actual lowering of the sea bottom under the weight of sediments, or from both. Subsidence of the bottom of the Java Sea almost certainly occurred in the Pleistocene. The distinctly marked drowned river valleys in the South China Sea trail across bottom that in places is deep-

er than 100 meters. If these former rivers are Pleistocene in age, then the net change in level of the South China Sea, between the low level of the Pleistocene and the high level of today, is greater than 100 meters.

Though Borneo has had intimate land connections with the Malay Peninsula and Sumatra during the Cenozoic, it has evidently had no subaerial connections with Celebes since the Mesozoic. Isthmian connections with the Philippine Islands were probably effected during the Pleistocene eustatic changes in sea level.

Climate.—Biologically, the most significant characteristics of the climate of Borneo are its constantly high temperature and its heavy, well-distributed rainfall. At low elevations (less than 1000 m.) the mean monthly temperature never falls below 20° C and rarely rises above 27.5° C. The annual amplitude of monthly means is usually

FIG. 3. Pleistocene drainages in Sunda area. Adapted from Umbgrove (1949).

much narrower than that. At Sandakan (5°54′ N, 118°05′ E), in the northeastern corner of the island, the monthly mean temperature varied between 26.1° and 27.2° C in the period 1953–58. The absolute extreme temperatures recorded during that interval were 18.3° and 35.5° C. At Kuching (1°29′ N, 110°20′ E), at the western end of the island, monthly means in the period 1955–60 varied from 24.8° to 27.5° C. Absolute extremes were 18.2° and 35.8° C.[1]

Temperatures in these coastal and near coastal cities approximate those of large clearings in interior forests (Inger and Chin, 1962, p. 21). Temperatures within the forests do not reach the extremes of the clearings. Temperature ranges two meters above ground over a 7-day interval (June, 1956) in rain forest at Kalabakan, Sabah, were 21.1° and 28.9° C. The corresponding figures in the adjacent camp clearing were 21.1° and 35.6° C. The extreme temperatures 1.5 m. above ground over a one-year interval in rain forest in the Third Division, Sarawak, were 20.4° and 30.8° C.

Rainfall over most of Borneo exceeds 2540 mm. (100 inches) per year and in some places may be twice that amount. Precipitation is well distributed over the year though not uniformly. The northeast monsoon (October to January) brings heavier rains to the eastern parts of the island, and the southwest monsoon (May to September) brings more rain to the western areas. Occasionally a month may have as little as 50 mm. of rain locally. As a general rule, however, very few places in Borneo have as much as one month per year with less than 100 mm. of rain. Consequently, there is no truly dry season, though, because of the shifting monsoons, it is usual for the rains to be heavier in one part of the year than in another. At Kuching, for example, the period December through February usually has the most precipitation and June-August the least (fig. 4).

In regions of such heavy rains, the relative humidities are correspondingly high. The mean monthly relative humidity at 14:00 hrs. at Sandakan varies between 67 per cent and 77 per cent; at 06:00 hrs. the range of monthly means is 91–93 per cent (Richards, 1952, p. 144). In the forests the humidity is somewhat higher.

The contrast between the climate of Borneo and those of Bangkok (13°45′ N) and of Chicago (41°47′ N) emphasizes the two meteorological factors that make one area suitable for tropical evergreen rain forest and others not (fig. 4). Though Bangkok is also in the tropics, precipitation is less than 100 mm. per month—the minimum tolerated

[1] Data from Summary of Observations 1953-1960, Malayan Meteorological Service, Singapore

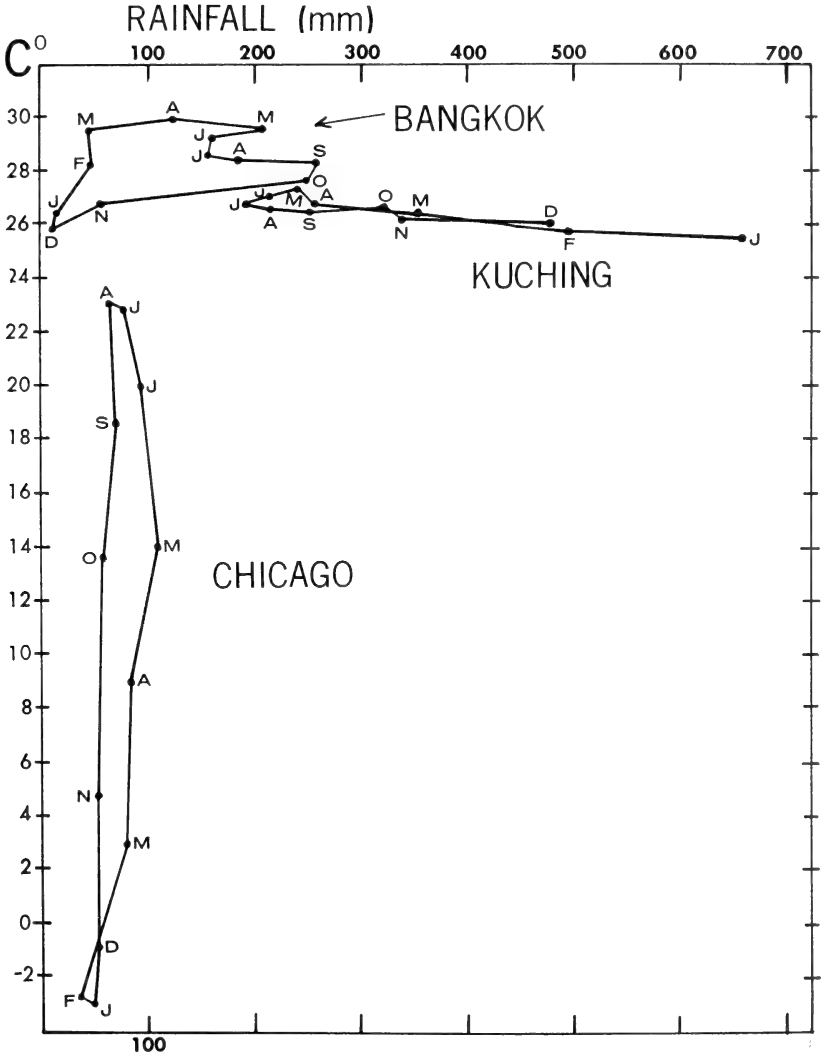


FIG. 4. Mean monthly temperatures and rainfall in continuously humid tropics (Kuching), in seasonally dry tropics (Bangkok), and in continental temperate zones (Chicago). Data for Bangkok and Chicago from World Weather Records (1941–50), Weather Bureau, U. S. Dept. of Commerce. Rainfall data for Kuching from Seal (1958, Sarawak Mus. Jour., 8, pp. 500–544). Temperature data for Kuching from Malayan Meteorological Service.

FIG. 5. Aerial view of hilly rain forest in eastern Sabah. Photograph by D. Dwight Davis.

by tropical rain forest (Richards, 1952)—for more than one-third of the year. Chicago has only one month above this rainfall tolerance threshold and many months below the usual mean temperature tolerance (18°–20° C) for lowland tropical rain forest. At Kuching, Sarawak, the minimum monthly rainfall is 190 mm. and the minimum mean monthly temperature is 25.5° C, both values well within the limits tolerated by tropical evergreen rain forest.

Vegetation.—Virtually the entire island of Borneo was covered with forest prior to settlement by man. As recently as 1957, approximately 75 per cent of Borneo was still covered by essentially primary forest (Smythies, 1957). The remainder is mostly in secondary growth as a result of primitive shifting agriculture, though some land is in permanent plantations of rubber, pepper, and copra, and some occupied by villages, towns, and cities. The amount of land affected by shifting agriculture has increased rapidly in the last 15 years.

The flat deltas are covered by mangrove and nipa palm which extend inland as far as brackish surface water. From that point to about 1000 m. above sea level, evergreen tropical rain forest (fig. 5) is the characteristic vegetation.[1] Though varying greatly because of edaphic and topographic factors, this forest generally has a closed canopy between 30 and 65 m. above the ground. The vegetation consists of several more or less distinct layers typical of tropical rain forests. Undergrowth varies from sparse to moderately thick depending mainly on the density of the canopy, which in turn varies with soil and slope characteristics.

Tree trunks in low, flat areas are commonly covered with moss. Epiphytes, principally orchids and ferns, are abundant everywhere, but do not generally hold reservoirs of water.

The higher mountains bear montane forests, also evergreen, but lower in stature and often richer in epiphytes and mosses (Richards, 1952, p. 347 ff.).

[1] These forests are described and analyzed in detail by Richards (1952).

SYSTEMATICS

KEY TO FAMILIES OF BORNEAN AMPHIBIANS

1A. Limbs absent . . . . Caeciliidae (p. 352).
B. Limbs present . . . . 2.

2A. No maxillary teeth . . . . 3.
B. Maxillary teeth present . . . . 4.

3A. Epicoracoids overlapping in mid-line . . . . Bufonidae (p. 53).
B. Epicoracoids not overlapping . . . . Microhylidae (p. 116).

4A. Sacral diapophyses expanded . . . . 5.
B. Sacral diapophyses cylindrical . . . . 6.

5A. Epicoracoids overlapping in mid-line . . . . Pelobatidae (p. 17).
B. Epicoracoids not overlapping . . . . Microhylidae (p. 116).

6A. An intercalary cartilage present between last two phalanges. Rhacophoridae (p. 279).
B. No intercalary cartilage . . . . Ranidae (p. 156).

KEY TO FAMILIES OF BORNEAN TADPOLES

1A. Spiracle median . . . . Microhylidae.
B. Spiracle sinistral . . . . 2.

2A. No transverse rows of labial teeth . . . . 3.
B. Lips with transverse rows of teeth . . . . 4.

3A. Lips expanded . . . . Pelobatidae (part).
B. Lips not expanded . . . . Ranidae (part).

4A. Papillae around entire margin of oral disk, at most a narrow gap in middle of upper lip . . . . Pelobatidae (part).
B. Papillae of upper lip confined to lateral quarters . . . . 5.

5A. Anal tube median . . . . 6.
B. Anal tube to right of midline . . . . 7.

6A. A large suctorial disk involving most of ventral surface of body Ranidae (part).
B. No such disk . . . . Bufonidae.

7A. Anal tube reaching margin of ventral fin . . . . Ranidae (part).
B. Anal tube not reaching margin of ventral fin . . . . Rhacophoridae.

PELOBATIDAE

Three genera have been reported from the Indo-Malayan area: *Megophrys* (widespread in the region), *Nesobia* van Kampen (Great Natuna Island), and *Leptobrachella* Smith (Borneo).

The species that in the most recent reviews (e.g., van Kampen, 1923; Smith, 1930; Bourret, 1941) have been grouped in the genus *Megophrys* were placed in three genera by Boulenger (1882): *Xenophrys* Günther (type *monticola* Günther=*Megophrys parva* Boulenger), *Megophrys* Kuhl (type *monticola* Kuhl), and *Leptobrachium* Tschudi (type *hasselti* Tschudi). Boulenger later (1908) lumped all three into the genus *Megophrys* because the characters by which he had previously separated them—presence or absence of vomerine teeth and type of vertebrae—varied intraspecifically.

Beddard (1907) not only maintained Boulenger's original division, but also established a fourth genus, *Pelobatrachus,* for the form *nasutus* Schlegel. Beddard had available only one specimen each of the type species of each of these "genera." Thus he could have had no basis for evaluating the differences he observed. As shown below, two of the forms Beddard examined (*monticola* Kuhl and *nasuta* Schlegel) are not even distinct species, let alone distinct genera.

Although genera cannot be maintained in this group on the basis of the characters used by Boulenger in 1882, previous workers (e.g., Smith, 1930; Pope, 1931) have called attention to the two sharply different types of larvae in the genus *Megophrys,* thus suggesting another basis for division. The larvae having so-called funnel mouths (fig. 6A), such as those of *boettgeri* and *brachykolos,* lack horny beaks and the usual horny labial teeth (fig. 6C). They also have in common median anal tubes that may be entirely free of the ventral fin (e.g., *monticola nasuta,* fig. 7B), free of the ventral fin near the end of the anal tube (e.g., *brachykolos*), or attached to the fin for the entire length of the tube (e.g., *minor*).

The other type of larva (fig. 6B) has a ventral, subterminal oral disk having rows of horny labial teeth and horny beaks (fig. 6D). The anal tube in these larvae is dextral and is firmly attached to the ventral fin (fig. 7A).

Adults of these two series differ consistently in several characters, the most conspicuous difference (and the one most helpful for rapid identification) involving the form of the inner palmar tubercle or pad. In species of *Leptobrachium* (forms with "normal" tadpoles) the inner palmar tubercle is circular, conspicuously elevated, and does not ex-

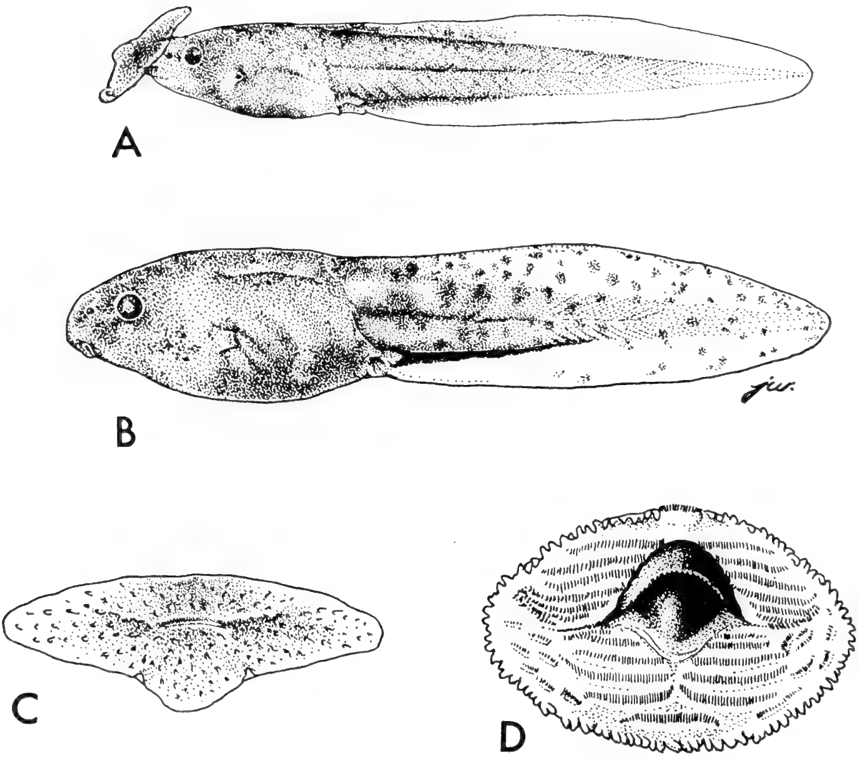


FIG. 6. Two types of Oriental pelobatid larvae. A, Tadpole of *Megophrys minor*, with "funnel" lips unfurled (× 1.2). B, Tadpole of *Leptobrachium hasselti* (× 1.4). C, Enlarged oral disk of *M. minor*. D, Enlarged oral disk of *L. hasselti*.

tend out along the first metacarpal (fig. 8C). In species of *Megophrys* (*sensu stricto*; forms with funnel-mouthed tadpoles) the inner palmal tubercle is oval, usually not elevated, and extends out along the first metacarpal (fig. 8D). Other differences are given in the following diagnoses.

Leptobrachium: adults with oval or circular, flat axillary glands posterior to arm; inner palmar tubercle circular, not extending along first metacarpal; a large circular sesamoid bone in palmar aponeurosis; squamosal without posterior otic projection; vomerine teeth absent; snout not projecting; dermal palpebral projections absent; ova pigmented or not. Larvae with ventral, subterminal oral disks; oral disk not transversely elongated; horny beaks present; horny labial teeth present; anus dextral, tube united to ventral fin (fig. 7A).

Species examined: *hasselti, gracilis, pelodytoides, oshanensis,* and *nigrops.*

Megophrys: adults with conical, teat-like axillary gland medial to arm; inner palmar tubercle oval, extending along first metacarpal; no sesamoid bone in palmar aponeurosis, sometimes a small nodule of

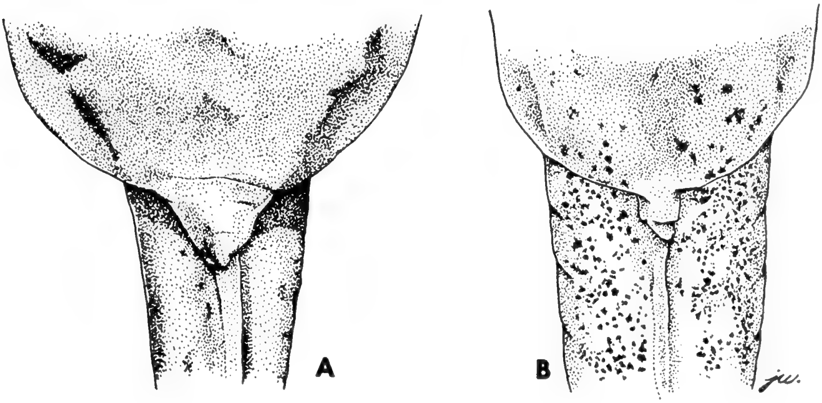


FIG. 7. Enlarged ventral view of root of tail of larvae of *Leptobrachium hasselti* (A), and *Megophrys monticola nasuta* (B).

cartilage present; squamosal with a posterior otic projection; vomerine teeth present or absent; snout usually projecting; small or large dermal palpebral projections usually present; ova non-pigmented. Larvae with terminal oral disks; oral disk transversely elongated; no horny beaks or labial teeth; anus median (fig. 7B), tube united to ventral fin or not.

Species examined: *monticola monticola, m. nasuta, m. ligayae, m. stejnegeri, boettgeri, minor, brachykolos, kuatunensis, baluensis, feae, shapingensis, omeimontis, longipes, lateralis,* and *parva* (only adults of last seven).

Characters other than those mentioned in the diagnoses have been said by other workers to distinguish between these two groups. For example, Beddard (1907) stated that *Leptobrachium hasselti* lacked hypopharyngeal processes (esophageal processes in the terminology of Trewavas, 1933) on the cricoid laryngeal cartilages, whereas *Megophrys monticola* and *M. parva* (= *Xenophrys monticola* of Beddard) had them. Two *L. hasselti* (FMNH 119893 from Borneo and FMNH 50919 from Mindanao) dissected in the course of this study have well-developed esophageal processes on the cricoids. Similar structures

were seen in *Leptobrachium gracilis* (FMNH 77213) and *L. pelodytoides* (FMNH 24416) and in *Megophrys monticola nasuta* (FMNH 67345) and *M. brachykolos* (FMNH 69064).

In conversation, Dr. E. H. Taylor suggested to me that the shape of the tongue differs in *Leptobrachium* and *Megophrys*. Anteriorly the tongue may widen immediately behind the symphysis of the mandible or only after a short but distinct narrow stem or stalk; the rear margin of the tongue may be notched or entire. All combinations of anterior and posterior lingual shape occur in the species examined (see lists above). The species of *Leptobrachium* have notched tongues usually lacking an anterior stem; *nigrops*, however, has a distinct stem. Most of the species of *Megophrys* (*sensu stricto*) examined have stalked tongues but *shapingensis* and *kuatunensis* do not. The rear margin of the tongue is notched in some species of *Megophrys* (*parva, lateralis*), entire in others (*monticola, baluensis, brachykolos*), and variable in others (*boettgeri, omeimontis*). Liu (1950, fig. 59) illustrates a stalked, entire tongue in *omeimontis* and a notched, stalked tongue in *shapingensis* (fig. 40); on every other basis these two species must be placed in the same group.

In summary, *Leptobrachium* and *Megophrys* differ in adult and larval morphologies. Adults of both are usually terrestrial and seem to have similar modes of life. The larvae, however, show a pronounced divergence in niche. Those of *Megophrys* are highly specialized for feeding on plankton in the surface film, whereas those of *Leptobrachium* have the benthonic feeding habits of anuran larvae in general.

Leptobrachella was differentiated from *Megophrys* and *Leptobrachium* (considered as one genus) by Smith (1925B) on the basis of its "more rudimentary sternal apparatus and shape of the digital extremities." The omosternum was described by Smith as cartilaginous and short. In the three *Leptobrachella* I dissected the omosternum is minute and simple. In *Leptobrachium* and *Megophrys* the omosternum is well developed and has an anterior expansion. The tips of both fingers and toes of *Leptobrachella* bear pointed, dilated disks (fig. 8A); the modified ventral skin of these disks is sharply delimited. Though *Leptobrachium* and *Megophrys* may have slightly swollen digital tips, the ventral surface of these swellings is not sharply set off from the rest of the digit. The digital disks of *Leptobrachella* are clearly more advanced.

Nesobia evidently was based on Günther's description (1895) of *Leptobrachium natunae*; at least van Kampen (1923) did not indicate that he had seen any material. The sole difference between *Nesobia*

and *Megophrys* given by van Kampen (1923) is in the shape of the pupil, which was said by van Kampen to be horizontal in *Nesobia* and vertical in *Megophrys*. However, Günther (1895) said that the shape of the pupil in *natunae* was uncertain; in one specimen it seemed to be horizontal and in another "produced upward into an angle."

The types of *Nesobia natunae* agree with *Leptobrachella* in the form of the digital disks and pectoral girdle. Though the Bornean species, *Leptobrachella mjobergi*, is specifically distinct from *natunae*, they clearly are members of the same genus not only sharing the above characters, but also those mentioned in the next paragraph. *Nesobia* is the prior name.

In other characters *Nesobia* is almost intermediate between *Megophrys* and *Leptobrachium*. Like the latter, *Nesobia* has a palmar sesamoid ossicle, an elevated inner palmar tubercle that does not extend out along the first metacarpal, and a squamosal lacking an otic projection. Like *Megophrys*, *Nesobia* has a teat-like gland medial to the axilla. The ova of *Nesobia* are non-pigmented as in all *Megophrys* and some *Leptobrachium*. *Nesobia* lacks vomerine teeth and a projecting snout as do all *Leptobrachium* and some *Megophrys*.

Little is known of the habits of *Nesobia*, but its specialized digital disks and the habit of the Bornean form of calling from low vegetation suggest that it is less terrestrial than *Leptobrachium* and *Megophrys*.

Leptobrachium appears to be the most generalized of the Megophryninae, and, therefore, probably the most primitive. The tadpole is similar to those of the Temperate Zone megophrynine genera, *Oreolalax*, *Scutiger*, and *Vibrissaphora*, and to those of the Pelobatinae. In the form of the inner palmar tubercle, the presence of a palmar sesamoid ossicle, and position and form of the axillary gland, *Leptobrachium*, *Oreolalax*, and *Vibrissaphora* are alike. The last two differ from *Leptobrachium* in having a ligamentous union of the quadratojugal and maxilla and in the development of heavy, spinose, male secondary sex characters. These sex characters are probably part of the adaptation of the Temperate Zone genera to breeding in swift, montane streams.

The differences between the Temperate Zone genera and *Leplobrachium* are carried one step farther by some species of *Scutiger* (e.g., *mammata*) in which the spines of the males are even heavier and in which the quadratojugal is entirely ligamentous. The loss of ossification in the quadratojugal is part of the general weakening of the jaw,

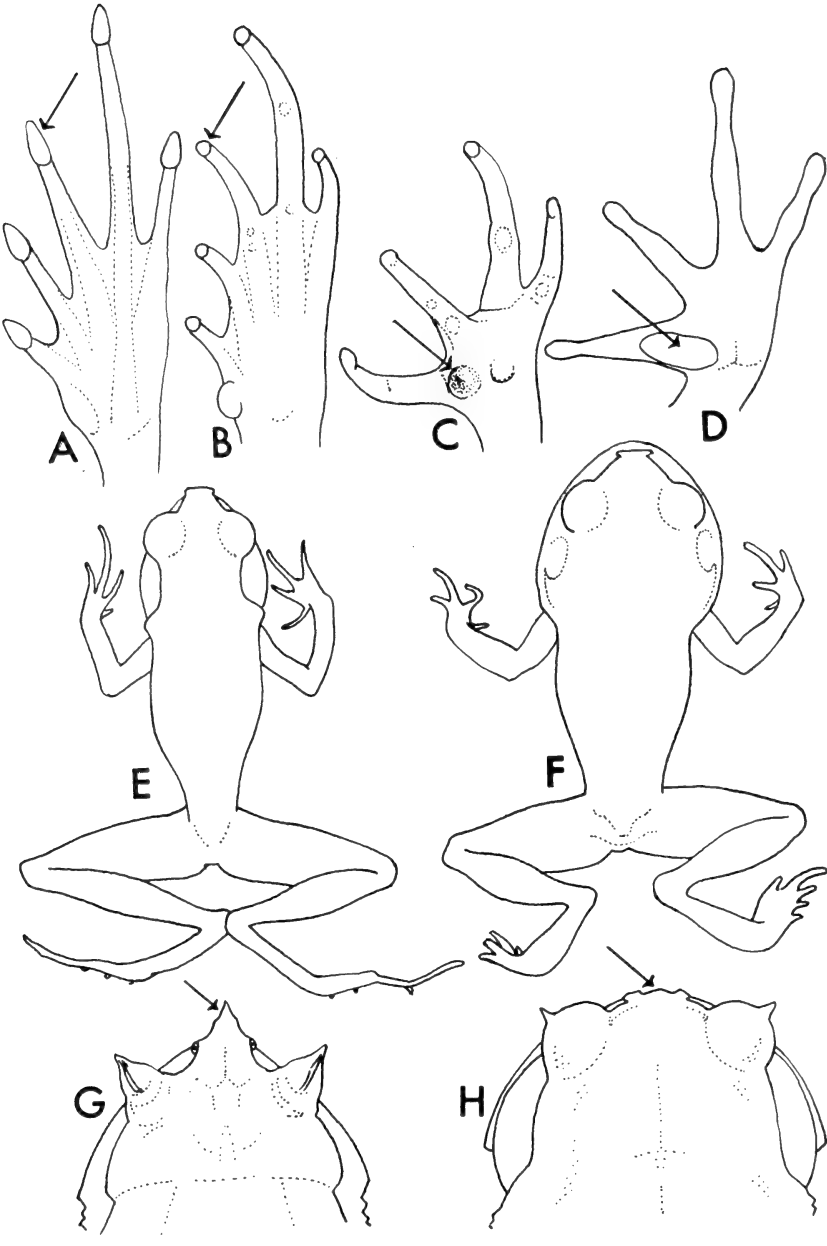


FIG. 8. Characters of Bornean pelobatids. See key for explanation.

to which Liu (1950, p. 119) referred; loss of maxillary teeth is probably part of the same specialization.

Scutiger usually lacks a palmar sesamoid ossicle, has a low inner tubercle, and usually lacks a post-axillary gland. In all these characters it differs from *Vibrissaphora, Oreolalax,* and *Leptobrachium.* According to Liu (1950), *Scutiger* (*Aelurophryne* in Liu's usage) is more aquatic as an adult than *Vibrissaphora* or *Oreolalax.* The most aquatic bufonid, *Pseudobufo,* has undergone reduction in ossification (Tihen, 1960) analogous to that of some *Scutiger.*

Scutiger represents one extreme of specialization in the Megophryninae. *Megophrys* (*sensu stricto*)—with its modified palmar tubercle loss of palmar sesamoid bone, the teat-like pectoral gland, and especially its specialized tadpole—represents the other extreme.

Nesobia apparently is an offshoot of the stock that ultimately gave rise to *Megophrys.* These two genera are alike in having teat-like, medial pectoral glands. The digital disks of *Nesobia* indicate that it is another extreme of specialization in the subfamily.

KEY TO BORNEAN PELOBATIDAE (Fig. 8).

1A. Tips of digits swollen, with pointed disks (fig. 8A); size never greater than 30 mm. . . . . *Nesobia mjobergi.*

B. Tips of digits usually not dilated, if swollen always rounded (fig. 8B); adults always larger than 30 mm. . . . . 2.

2A. Inner palmar tubercle elevated, round, not extending out first finger (fig. 8C). 3.

B. Inner palmar tubercle low, oval, extending out first finger (fig. 8D) . . . . 5.

3A. Head not much wider than body (fig. 8E); length of tibia greater than width of head . . . . *Leptobrachium gracilis.*

B. Head conspicuously wider than body (fig. 8F); length of tibia less than width of head . . . . 4.

4A. Tips of fingers sharply pointed; maximum size of adults about 50 mm. *Leptobrachium nigrops.*

B. Tips of fingers rounded; adults usually larger than 50 mm. *Leptobrachium hasselti.*

5A. Snout very short, without dermal projection (fig. 8H) . . . *Megophrys baluensis.*

B. Snout moderate, usually with conspicuous dermal appendage (fig. 8G) *Megophrys monticola nasuta.*

KEY TO KNOWN TADPOLES OF BORNEAN PELOBATIDAE

1A. Lips directed upward to form a wide funnel (as in fig. 6A, C) *Megophrys monticola.*

B. Lips directed downward . . . . 2.

2A. Well-developed rows of teeth extending across width of lips (fig. 6D) . . . . . . 3.

B. Feeble rows of teeth not more than one-fifth width of lips (fig. 9) *Leptobrachium gracilis.*

3A. A wide black band across root of tail...... *Leptobrachium nigrops* (tentative).

B. With large or small black spots, but never with broad band across base of tail *Leptobrachium hasselti.*

Leptobrachium Tschudi

Leptobrachium gracilis Günther

Leptobrachium gracile Günther, 1872, Proc. Zool. Soc. London, **1872**, p. 598—Matang, Sarawak; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 440.

Megalophrys gracilis Boulenger, 1908, Proc. Zool. Soc. London, **1908**, p. 421, pl. 25, fig. 1; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 15; Smith, 1925, Sarawak Mus. Jour., **3**, p. 14.

Megophrys gracilis Smith, 1930, Bull. Raffles Mus., no. 3, p. 133; *ibid.*, no. 5, p. 12.

Material examined.—Borneo 69+10 series of larvae (4 BM, including holotype; 54+9 series of larvae FMNH; 4 MHNP; 2 RMNH; 5+series of larvae SM); Malaya 2 (BM).

Description.—A small species, males 30–36 mm., females to ca. 50 mm.; head and body slender (fig. 8E); head longer than wide, width 0.29–0.33 of snout-vent (median 0.314; N = 11); snout obtusely pointed, not projecting; eye large, diameter equal to or longer than snout; interorbital narrower than upper eyelid, equal to eye-nostril distance; canthus rostralis distinct, straight; lores oblique, concave; tympanum distinct, about one-half diameter of eye; no vomerine teeth.

Tips of fingers rounded, not swollen; terminal phalanges pointed; first, second, and fourth fingers subequal; large, inner palmar tubercle not extending on to first metacarpal and a small outer one; subarticular tubercles absent, their places taken by long strips of callous tissue forming low ridges. Tips of toes like those of fingers; third toe longer than fifth; toes webbed at bases; third toe with 2⅔ to 2¾ phalanges free of web, fifth with 2⅔ to 3 free; inner metatarsal tubercle low, longer than distance between subarticular tubercle and tip of first toe; no outer metatarsal tubercle; large subarticular tubercles on first and second toes, those of outer toes replaced by distinct ridges of callous tissue; tibia 0.45–0.55 of snout-vent (median 0.508; N = 13).

Skin above smooth or with a few small tubercles; skin below smooth or weakly rugose at rear of abdomen; a low supratympanic ridge from eye to axilla; a flat, round glandular area mesad from axilla; no femoral gland.

Color (in alcohol) dark gray or brown above, usually with irregular black spots each longer than diameter of tympanum; a black interorbital bar or triradiate marking usually present; lips barred with black; underside of head and body white, spotted with black; dorsal surface of thigh with black crossbars; tibia with black spots along sides, rarely continuous as bars across dorsal surface.

Secondary sex characters.—The three adult males seen measure 32.1–36.2 mm. (mean 33.8); the ten females containing enlarged ova measure 40.3–51.3 mm. (mean 43.43 ± 0.34).

The males lack nuptial pads and lineae masculinae, but have median, subgular vocal sacs that are constricted in the mid-ventral line. The round vocal sac openings are located in the floor of the mouth posterior to the rictus and close to the openings of the eustachian tubes.

Larvae and development.—Ten lots of tadpoles (fig. 9) adapted to swift currents are assigned to this species. All have the completely fringed upper lip characteristic of pelobatid larvae as well as sinistral

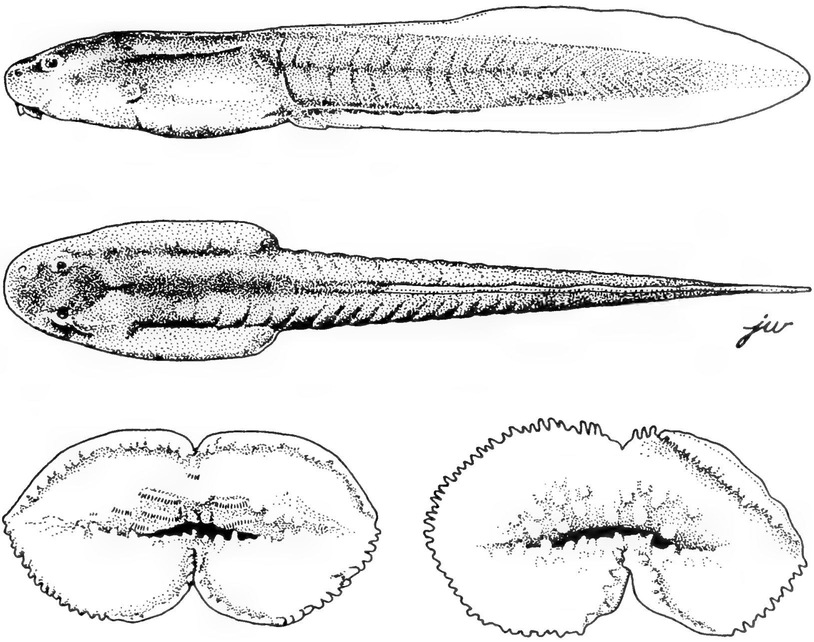


FIG. 9. Tadpole of *Leptobrachium gracilis*. Bottom row, enlarged view of oral disks showing presence (left) and absence (right) of rows of labial teeth.

spiracles and dextral vents. Three tadpoles (FMNH 77509, 130860) in early metamorphic stages (XX) have the deep lips of younger larvae and two have papillae still present; their toes have the peculiar callous ridges typical of adult *gracilis*. The developmental series is completed by three specimens (FMNH 63489, 77217, 77219) in late metamorphic stages; their mouths are adult in form, they have partially resorbed tails, and they are certainly conspecific with the other metamorphosing specimens and with adult *gracilis*.

Description of premetamorphic larvae: Body elongate, about twice as long as wide; eyes dorsal, not visible from below, diameter equals one-fourth to one-third of eye-nostril distance; nostrils dorsolateral, closer to tip of snout than to eye; internarial distance subequal to eye-nostril and to interorbital; oral disk ventral, about three-fourths width of head; lips expanded, hanging to form a deep cup in preserved specimens; both lips notched in center, the lower one more deeply; one row of short, closely spaced papillae around entire margin of oral disk; both beaks strong, completely black, margins serrate; labial teeth discussed below; an oblique row of low papillae along outer borders of labial teeth.

Spiracle sinistral, tubular, opening above mid-line of side, distance between eye and spiracle about 1¾ times in distance between spiracle and root of hind limb buds; vent dextral, opening near edges of ventral fin.

Total lengths 25.0–47.0 mm.; tail 0.57–0.69 of total length; tail lanceolate, margins subparallel, tapering rather abruptly near end to rounded tip; caudal muscle heavy, deeper than fins except in distal third; dorsal fin beginning well behind body, subequal to depth of ventral fin; latter beginning at root of tail.

Color of head and body in alcohol light brown above, colorless below, immaculate; caudal muscle same color as top of head and body; fins pale dusky.

In life these tadpoles are pinkish brown and can scarcely be noticed amongst the similarly colored pebbles of the stream bottom. Their slender form gives them a fish-like appearance.

These larvae are polymorphic in the structure of the oral disk (fig. 9, bottom). Though all have greatly expanded, cup-like lips, only some have labial teeth. Weak labial teeth appear in only seven of 25 premetamorphic larvae. All seven are in pre-limb bud stages or in Stage I. The dental formulae for the upper lip varies from I: 2-2 to I: 5-5, those for the lower lip from 2-2: I to 3-3: I. All tooth rows

are short (less than one-fifth width of oral disk) and halves of divided rows are widely separated.

The 18 lacking labial teeth vary in development from pre-limb bud to Stage XI. They have two or three transverse rows of low papillae

TABLE 1.—Variation in the ratio of eye diameter to head-plus-body length in larvae of *Leptobrachium gracilis.*

Locality	Head-plus-body (mm.)	Developmental stage	Eye ratio
North Borneo	10.5	prelimb bud	0.038
"	10.8	" "	0.027
"	10.9	" "	0.027
"	11.1	' "	0.036
"	11.1	" "	0.036
"	11.9	" "	0.033
Sarawak	12.8	" "	0.054
"	13.1	" '	0.045
North Borneo	13.3	" "	0.037
"	13.9	" "	0.035
Sarawak	18.3	Stage I	0.038
"	13.4	Stage V	0.052
North Borneo	12.5	Stage VI	0.056
Sarawak	13.0	Stage IX	0.092
North Borneo	11.7	Stage X	0.068
"	12.0	Stage XI	0.083
Sarawak	16.9	Stage XX	0.118
"	17.3	"	0.121

crossing the central portion of each lip. The outer-most rows of these papillae resemble those flanking the labial teeth of other individuals.

In those tadpoles lacking teeth, apparently the central papillae represent fragments of the ridges that in the other tadpoles bear the labial teeth. This suggestion is supported by the presence of infra-marginal papillae in the individuals having labial teeth, by the feeble development of labial teeth whenever they appear in this species, and by the frequent breaks in the rows of labial teeth.

The ratio of eye diameter to head-plus-body length in the larvae varies from 0.027–0.121 (Table 1). Though correlation of the ratio with head-body length is not close, the eye is proportionately larger in larvae in which the hind limb has begun to develop.

In the form of the oral disk and body shape, this tadpole resembles those of *L. oshanensis* Liu (1950) and *L. pelodytoides* (Smith, 1917), except that the dental ridges of *gracilis* larvae are shorter.

Ecological notes.—Fifty-one of the 52 transformed frogs for which data are available were caught in primary rain forest and one in old

secondary growth. Most adults were collected at night either along stream banks (10 specimens) or on the forest floor away from streams (3); three were caught during daylight hours under leaves on the forest floor. Most juveniles were caught by day under leaves (30) or exposed on the forest floor (1); only three were obtained at night, two on stream banks and one on the forest floor.

Larvae were collected in small, clear, shallow streams having moderate to strong currents and beds of sand, gravel, and rock. I did not see these tadpoles alive, but judging by their unusually slender bodies and deep, cup-like lips, they seem to be adapted to wriggling amongst and clinging to pebbles in mid-current. In similar streams in China, Liu (1950) found the very similar larvae of *Leptobrachium oshanensis* hiding between or under rocks.

The altitudinal range of *gracilis* in Borneo extends from near sea level (less than 100 meters) to 2195 meters, 11 of the adults seen coming from less than 150 meters above sea level. Only two have been caught above 2100 meters. In Malaya *gracilis* has been taken at 1585 meters (Boulenger, 1912).

Geographic variation.—The frogs reported by Boulenger (*ibid.*) from Gunong Tahan, Malaya, have smaller dorsal spots and rounder inner metatarsal tubercles than those from Borneo. The mid-dorsal spots of the Malayan specimens are much less than half the diameter of the eye whereas those of Bornean frogs are usually longer than half the eye diameter. The metatarsal tubercle is more than twice as long as wide in Bornean frogs and only slightly longer than wide or as wide as long in the Malayan frogs.

The two from Malaya, one with a vestige of the tail stump and one with a 13 mm. partially resorbed tail (the mouth is adult in form), are larger (28.1 and 29.0 mm.) than three from Borneo (17.2–21.6 mm.) having partially resorbed tails (5.5–10 mm.).

Range.—Malaya and Borneo.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Kota Belud District, Kiau (Smith, 1931), Kamboranga on Mount Kina Balu; Ranau District, Sungei Kepungit, Sungei Mamut, Sungei Liwagu; Tawau District, Kalabakan. SARAWAK: First Division, Matang, Mount Penrissen; Third Division, Baleh River near mouth of Sungei Putai, Mengiong River; Fourth Division, Sungei Paloh in Patah valley, Tutoh River valley; Fifth Division, Mount Murud. KALIMANTAN: Mahakam River valley.

Leptobrachium hasselti Tschudi

Leptobrachium hasselti Tschudi, 1838, Mem. Soc. Sci. Nat. Neuchatel, **2**, p. 81—Java.

Megalophrys hasselti Boulenger, 1908, Proc. Zool. Soc. London, **1908**, p. 425; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 13; Smith, 1925, Sarawak Mus. Jour., **3**, p. 14.

Megophrys hasselti, Smith, 1931, Bull. Raffles Mus., no. 5, p. 30; Inger, 1954; Jour. Washington Acad. Sci., **44**, p. 250; 1956, Fieldiana, Zool., **34**, p. 393.

Megophrys abbotti Cochran, 1926, Jour. Washington Acad. Sci., **16**, p. 446—Balikpapan, Borneo.

Leptobrachium hendricksoni Taylor, 1962, Univ. Kansas Sci. Bull., **43**, p. 308, fig. 9—Bhetong, Yala, Thailand.

Material examined.—Borneo 182+35 series of larvae (164+larvae FMNH; 6 MCZ; 6 RMNH; 1 SM; 1 UNMZ; 4 USNM, including type of *abbotti*); Java 18 (5 BM; 9 NHMW; 3 RMNH; 1 USNM); Mindanao 11 (9 FMNH; 2 USNM); Palawan 6 (4 FMNH; 2 MCZ); Malaya 14 (1 BM; 11 FMNH; 2 ZMB); Burma 4 (NHMW).

Taxonomic notes.—Cochran (1926) stated that *abbotti* differed from *hasselti* in lacking a dorsal pattern and in having a "very distinct" tympanum, the nostrils at the end of the upper surface of the snout, and a sloping, truncate snout. These characters do not differentiate *abbotti* from *hasselti*. All Bornean specimens examined agree with the holotype of *abbotti* and are conspecific with it.

The Bornean frogs differ from those of Java (type locality of *hasselti*), northern Thailand (Taylor, 1962) and Burma in lacking conspicuous, black, dorsal markings. Bornean frogs have at most an obscure, dark, interorbital triangle and, more rarely, a few black spots ventrolaterally; in general, the Bornean frogs appear uniform dark blackish or purplish brown. Mindanao and Palawan frogs resemble those from Borneo in coloration.

Slight but statistically significant differences in body proportions distinguish the Bornean population from those of Java and Burma (Table 2). In the ratio of tibia to snout-vent only two of 20 males from Borneo and Mindanao fall below 0.363, whereas five of six from Java and Burma and all four from Palawan do. In the head-width ratio two of 21 males from Borneo and Mindanao fall below 0.425, whereas five of six from Java and Burma and all four from Palawan do. In mature females the tibia ratio falls below 0.350 in only two of 10 from Borneo and Mindanao, in none of 2 from Palawan, but in all 11 from Java. The head-width ratio of females falls below 0.416 in one of 11 from Borneo and Mindanao, in one of two from Palawan, but in all 10 from Java.

TABLE 2.—Comparison of certain populations of *Leptobrachium* from Malaysia.

Form	Ratio of tibia to snout-vent[1] Males			Ratio of tibia to snout-vent[1] Females			Ratio of head width to snout-vent[1] Males			Ratio of head width to snout-vent[1] Females			Direction of pectoral gland from arm insertion	Labial teeth of larvae	
	No.	Range	Median	No.	Range	Median	No.	Range	Median	No.	Range	Median		Upper	Lower
hasselti:															
Java	4	352–370	360	11	306–349	330	4	405–439	426	10	369–415	396	posterior	I:5–5	5–5:I
Burma	2	330–357	343	2	347–360	354	2	410–411	411	2	382–416	399	posterior	—	—
Malaya	2	341–376	358	1	364	—	2	426–435	430	1	422	—	posterior	—	—
Borneo	13	357–387	370	8	333–395	360	14	414–477	437	10	407–462	437	posterior	I:5–5 or I:6–6	5–5:I
Mindanao	7	337–376	369	2	365–371	368	7	436–464	450	1	428	—	posterior	I:5–5 or I:6–6	5–5:I
Palawan	4	334–362	348	2	353–377	365	4	402–424	416	2	405–430	418	posterior	I:6–6	5–5:I
		$H^2=13.44$; $P=0.01$			$H^2=13.56$; $P=0.005$			$H^2=16.56$; $P=0.004$			$H^2=13.92$; $P=0.005$				
gracilis	3	508–551	539	9	449–530	504	3	309–333	318	7	285–333	314	mesad	I:2–2—5–5	2–2–3–3:I
nigrops:															
Malaya	—	—		7	348–393	368	—	—		9	350–395	381	posterior	—	—
Borneo	4	375–387	383	12	353–391	372	4	389–409	395	12	359–410	386	posterior	—	—

[1] In terms of thousandths of snout-vent length.
[2] Using Kruskal-Wallis analysis of variance (Siegel, 1956).

Taylor (1962) described a new species, *Leptobrachium hendricksoni*, on the basis of three frogs from southern peninsular Thailand and central Malaya. I have examined 16 Malayan specimens agreeing with the description of *hendricksoni*: two from Malacca, 13 from Kuala Lumpur, and one from Perak. Several samples totaling 72 specimens from four localities (Labang, Niah, Nyabau, and Tubau) in the Fourth Division, Sarawak, consist mainly of frogs identical to *hendricksoni*.

The principal differences between *hendricksoni* and *hasselti*, according to the information in Taylor's paper, are in ventral coloration (*hendricksoni* white with small black spots, *hasselti* whitish with dark reticulation), in dorsal coloration (*hendricksoni* without spots, *hasselti* with large dark spots), in the size of the axillary gland (larger in *hendricksoni*), in the development of the femoral glands (said to be diffuse in *hasselti*, concentrated into one or two clusters in *hendricksoni*), and in the rugosity of the ventral skin (*hasselti* granular, *hendricksoni* with indistinct flat tubercles posteriorly).

The dark dorsal coloration of *hendricksoni* is matched in all Bornean *hasselti* (see above). I can find no difference between the Malayan and Bornean samples in the size or shape of the axillary gland. The ventral skin varies from smooth to granular in both Bornean and Malayan samples; at least part of this variation is caused by accidents of preservation.

Most of the frogs from the Fourth Division, Sarawak, and all of those seen from Malaya, have a ventral pattern of small black dots on a whitish background. Except for recently transformed individuals, the Sarawak frogs have fewer spots than do the Malayan ones. Included in the Fourth Division samples are 14 (19%) that either lack ventral markings or have dark blotches. The last two types characterize the other 104 Bornean *hasselti* examined (from eastern Sabah, Kalimantan, and southern and western Sarawak).

The femoral gland in Bornean *hasselti* is concentrated in a single, large white area or is broken into two or more smaller white areas. Both conditions occur with each of the various types of ventral patterns. The frequency of a single, large gland in frogs having the dotted ventral pattern is 90%; it is only 38% in Bornean frogs having immaculate white or blotched venters.

Frogs having blotched or immaculate bellies have the rear face of the thighs dark. Those having dotted venters, whether from Malaya or the Fourth Division, Sarawak, have pale brownish or purplish thighs.

Larvae from the Malay Peninsula are dotted with black (Taylor, 1962, fig. 10), a pattern that is retained after metamorphosis except dorsally. The same coloration is found in larvae from the Sarawak populations having dotted venters. Elsewhere in Borneo, the larvae have large black spots on the tail and similarly spotted or uniformly dark bodies.

It is clear that a portion of the total Bornean population is very similar to Malayan *hendricksoni* in coloration and in form of the femoral gland. But the variation within several of the Bornean samples and the intergradation between Bornean samples in the only two characters—ventral coloration and femoral gland form—that distinguish the *hendricksoni*-type from the others show that *hendricksoni* is not a separate species. Certainly "*hendricksoni*" is not as distinct from *hasselti* of Java as either is from *L. gracilis* and *L. nigrops* (Table 2). In Borneo and Malaya *L. hasselti* is sympatric with *gracilis* and *nigrops* at a number of localities.

The appearance of two conspecific populations on Borneo, one of them very similar to a Malayan population, is not a unique situation. Analogous situations involve other amphibians (see *Megophrys monticola* below) and reptiles (Inger and Marx, 1965) in the Indo-Malaysian area.

The subspecies, *hasselti pullus* Smith (type locality Annam), was said to differ from the nominate form in its longer and more prominent metatarsal tubercle, its longer leg, and darker coloration (Smith, 1921A). The form from Tonkin, *hasselti chapaensis* Bourret, supposedly differs from the nominate form in its longer leg and longer metatarsal tubercles (Bourret, 1941). Burmese specimens (NHMW 6621) are darker than those from Java but are distinctly spotted. The tibio-tarsal articulations of Javan and Burmese frogs reach from the shoulder to the tympanum and thus span one of the supposed differences between *h. hasselti*, on the one hand, and *h. pullus* and *h. chapaensis* on the other. Similarly, variation in size and shape of the metatarsal tubercle in the Javan and Burmese series spans another supposed difference (Bourret, 1941) between *h. hasselti* and the other mainland forms. Recognition of subspecies of this wide-ranging frog must wait for more detailed analyses of large Javan and mainland samples.

Description (based on Bornean specimens).—A moderate to large-sized species, males 40–65 mm., females to ca. 90 mm.; head broad, body tapering (fig. 8F); limbs slender; head length and width subequal, head width 0.41–0.48 of snout-vent (Table 2); snout obtusely pointed or truncate, not projecting; interorbital wider than upper eye-

lid, greater than eye-nostril distance; canthus rostralis sharp; lores oblique, weakly concave; tympanum distinct, about half of eye diameter; no vomerine teeth.

Tips of fingers rounded, not swollen; terminal phalanges pointed; first and second fingers subequal, fourth shorter, third much longer; a large, round, inner palmar tubercle not extending on to first metacarpal, and a small outer one; subarticular tubercles replaced by low ridges of callous tissue. Tips of toes like those of fingers; third toe longer than fifth; toes about half-webbed; third toe with $2\frac{1}{3}$–$2\frac{1}{2}$ phalanges free; fifth toe with two phalanges free; inner metatarsal tubercle low, oval, about half distance between tip of first toe and tubercle; no outer metatarsal tubercle; subarticular tubercles replaced by low ridges of callous tissue.

Skin above smooth or with a network of low ridges; a supratympanic fold from eye to axilla; skin below weakly rugose or granular; a round, flat gland in axilla behind arm; a small, round femoral gland.

Color (in alcohol) dark brown or purplish gray above; an obscure interorbital black marking present or absent; usually a black stripe below the canthus and one below supratympanic fold; limbs with black dorsal bars or with lateral rows of black spots; rear of thigh usually marked with black; ventrally whitish, with large or small black spots.

Secondary sex characters.—Though the size range of each sex is extensive, females are definitely larger than males. Seven Bornean females containing enlarged, pigmented ova vary from 57.0–91.3 mm. (mean 74.28). All Bornean males ($N = 14$) larger than 43.4 mm. have vocal sac openings; the maximum snout-vent length is 66.9 mm., the mean 55.73.

Males have median subgular vocal sacs with openings behind the corners of the mouth. They lack nuptial pads or other asperities.

Larvae and development.—Tadpoles fitting the description of *hasselti* larvae (van Kampen, 1923; Smith, 1930) were among the commonest larvae found in small clear or slightly turbid forest streams. The collection includes all stages of development from pre-limb bud through metamorphosis.

Body deep, ovoid (fig. 6B); eyes dorsal, not visible from below; spiracle sinistral; anus dextral, opening at edge of ventral fin (fig. 7A); tail muscle strong, fins beginning at root of tail; margin of dorsal fin convex, fin deeper than muscle beyond middle of tail; margin of ventral fin weakly convex, fin half depth of dorsal fin; tail tapering to rounded tip.

TABLE 3.—Frequency distribution with respect to number of divided labial tooth rows in larval *Leptobrachium hasselti* from two areas of Borneo.

		Upper lip							Lower lip					
Stage	Area	4–4	4–5	5–5	5–6	6–6	6–7	7–7	3–4	4–4	4–5	5–5	5–6	6–6
Pre-limb bud														
5–9 mm.	Eastern Sabah	7	1	24					1	13	1	18		
10–15 mm.	Eastern Sabah		2	40	2	5			1	16	4	26	1	
10–15 mm.	Sarawak			3		1				2		1		1
16–26 mm.	Sarawak			2		2		3		1		1		5
I–XVIII	Eastern Sabah	1		69	21	86		2	1	5	8	158		2
I–XVIII	Sarawak			3		10	1	4		3	1	5		8

FIG. 10. Small rocky stream in primary forest. Characteristic habitat of larval *Leptobrachium hasselti* in Borneo.

Mouth ventral, subterminal; beaks heavy, serrate, black (fig. 6D); labial teeth usually I: 5–5/5–5: I or I: 6–6/5–5: I (see Table 3 for variation).

Color varies geographically (see *Taxonomic notes*).

Ontogenetic changes in dental counts and size are given in Tables 3 and 4. A specimen with forelimbs erupted and a complete tail measures 16.5 mm. snout to vent.

Ecological notes.—In Borneo *Leptobrachium hasselti* lives mainly in primary rain forest, though it is occasionally found in clearings. Of the transformed frogs for which I have detailed information, 156 were caught in primary rain forest, six in logged forest in which trees characteristic of primary forest were abundant, and one in a large clearing. Those from primary forest were found on stream banks or on the forest floor at some distance from water. Only 13 were caught by day, six of them on stream banks and four under leaves or logs. All larvae were collected in quiet reaches of streams (fig. 10), 29 series in primary forest, two in the same logged forest mentioned above, and four in secondary growth.

The altitudinal range of this species in Borneo is extensive, running from a few meters above sea level to 1825 meters (Smith, 1925A).

Most Bornean adults were caught below 300 meters above sea level, one at 300–600 meters, and seven above 900 meters. In the Philippine Islands *hasselti* occurs from near sea level to 1340 meters (Inger, 1954A). In Malaya this species occurs within 100 meters of sea level (Kuala Lumpur).

Larvae were collected in numerous small forest streams and were observed grazing on algae growing on rocks in clear water. In the laboratory they fed on dead leaves and dead tadpoles (Inger, 1956).

Bornean females having enlarged, pigmented eggs were caught in January, June, July, and August; these frogs were from scattered localities. Larvae in various stages were collected in April, June, and September in northern Sarawak, in February in southwestern Sarawak, and in May, June, and August in eastern Sabah. Probably *hasselti* breeds all year round in Borneo.

Geographic variation.—Larvae from Sarawak are larger than those from eastern Sabah (Table 4). As already noted, larvae from the Fourth Division, Sarawak, and from the Malay Peninsula are covered with numerous small black dots. Those from eastern Sabah have large black spots dorsally on the body and on the tail. Those from southern Sarawak have blackish bodies and light, black-spotted tails.

The Sarawak tadpoles tend to have more rows of labial teeth than do those from eastern Sabah. In this character the larvae from the Fourth Division do not differ from those from other parts of Sarawak.

TABLE 4.—Variation in head-plus-body length of Bornean larvae of *Leptobrachium hasselti*.

Stage	Eastern Sabah			Sarawak		
	N	range	mean	N	range	mean
Pre-limb bud	81	5–15	....[1]	11	13–26	....[1]
I–VI	126	11–18	14.5	8	17–27	22.6
VII–XII	28	16–21	17.9	6	24–34	28.0
XIII–XVIII	17	18–21	18.6	5	27–36	29.6

[1] Means not calculated as values are too easily biased by inclusion or exclusion of very young tadpoles.

Geographic variation in coloration and femoral glands has been discussed in the *Taxonomic notes*.

Range.—From Burma and Indo-China to Java, Borneo, and the Philippine Islands (to Mindoro in the west and Mindanao in the east).

SABAH: Kinabatangan District, Bukit Kretam; Kota Belud District, Kiau, Lumu Lumu; Ranau District, Bundu Tuhan, Sungei

Kepungit, Sungei Liwagu, Sungei Matukungan; Sandakan District, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tawau District, Kalabakan; Mount Kappa (van Kampen, 1923). SARAWAK: First Division, Gunong Temiang; Second Division, Lupar River Valley; Third Division, Baleh River near mouth of Sungei Putai, headwaters of Baleh River, Mengiong River; Fourth Division, Bario, Labang, Long Sinei, Niah, Nyabau, Sungei Pesu; Fifth Division, Mount Murud. KALIMANTAN: Gunong Kenepai, Liang Kubung, upper Mahakam River, Pramassan-Alai mountains (van Kampen, 1923).

Leptobrachium nigrops Berry and Hendrickson

Leptobrachium nigrops Berry and Hendrickson, 1963, Copeia, **1963**, p. 644, figs. 1–2—Nee Soon, Singapore.

Material examined.—Borneo 27 (FMNH); Malaya 13 (FMNH, including holotype and paratype).

Taxonomic notes.—Adults of a small species of *Leptobrachium* were caught at two localities in the Fourth Division, Sarawak. Snout-vent in females with mature oviducts measured 37.3–46.8 mm., almost identical to the range of Malayan *nigrops* (37.7–47.7). The Bornean frogs also agree with Malayan *nigrops* in head width and tibia length (Table 2) and in having a broad, black, horizontal band on the rear of the thigh. The Bornean frogs have a dorsal pattern of black spots as in *nigrops* (Berry and Hendrickson, 1963, fig. 1), but the pattern is often obscured by a dark ground color.

Tadpoles of two species of *Leptobrachium* were collected at both Bornean localities for *L. nigrops*. One species of tadpole is the black-dotted type of *L. hasselti* (see p. 32). The other, though having labial tooth counts similar to *hasselti* larvae (Table 2), differs strikingly in coloration (see below). The tadpole of the only other species of *Leptobrachium* known from Borneo, *gracilis*, has a grossly different body form and coloration (see p. 26). Consequently, the most likely parent of the questionable tadpole is *L. nigrops*. These Bornean larvae, however, do not agree with those assigned to Malayan *nigrops* (Berry and Hendrickson, 1963) in coloration or labial tooth counts. A Malayan larva (body length 13.5 mm.) has the dental formula 3–3/3–2:I and uniformly dark coloration (Berry and Hendrickson, 1963). Bornean larvae of comparable size have dental formulae of I:5–5/5–5:I and a light body with a broad, black saddle across the root of the tail.

The Malayan larvae were described as elongate and slender. This shape and the reduced number of dental rows recall the tadpole of *L. gracilis*. As Berry and Hendrickson did not rear eggs from known

parents, their identification must rest on newly metamorphosed frogs which are often difficult to identify. *Leptobrachium gracilis* and its relative *L. pelodytoides,* both of which occur in the Malay Peninsula, are spotted dorsally as is *nigrops*. The Malayan tadpoles may belong to an unknown relative of *L. gracilis*.

Identification of the Bornean larvae is equally uncertain, resting on the occurrence of adults and differences from known larvae.

The only certain distinction between the Bornean and Malayan adults is in the shape of the finger tips. Those of the Bornean frogs are sharply pointed and slightly hooked. In Malayan frogs they are narrow, but not pointed. The terminal phalanges are the same shape in both groups.

Description (based on Bornean specimens).—A small species, males less than 40 mm., females less than 50 mm.; head moderately broad; limbs slender; head wider than long, width 0.36–0.41 of snout-vent (Table 2); snout obtusely pointed, not projecting; interorbital equal to or narrower than upper eyelid; canthus rostralis sharp; lores oblique, weakly concave; tympanum partly obscured by skin, one-third to one-half diameter of eye; no vomerine teeth.

Tips of fingers not swollen, sharply pointed and often hooked; terminal phalanges pointed, straight; first finger equal to or larger than second, fourth shorter; inner palmar tubercle elevated, round, not extending on to first metacarpal; a smaller round outer palmar tubercle; subarticular tubercles replaced by low ridges. Tips of toes not as sharply pointed as tips of fingers, not swollen; third toe longer than fifth; third and fifth toes with two phalanges free of web; an oval inner metatarsal tubercle; no outer tubercle; underside of toes like those of fingers.

Skin above smooth or with a network of low ridges; a supratympanic fold from eye to axilla; skin below rugose or granular; a round, flat gland in axilla behind arm; a small femoral gland present or absent.

Color (in alcohol) purplish brown above, oval black spots on top and side of head and on back, obscured by dark ground color on back of some individuals; usually a black line or band below supratympanic fold; dorsal surface of thigh with narrow black crossbars; rear of thigh with irregular, horizontal black band; ventrally whitish with small black spots that tend to run together especially posteriorly and laterally.

Secondary sex characters.—The four Bornean males measured 35.4–36.8 mm. Females having enlarged, convoluted oviducts were larger,

37.3–46.8 mm. (N = 13). The slit-like vocal sac openings of the males are located far back in the mouth. Nuptial asperities are absent.

Larvae.—Reasons for the tentative identification of the tadpoles are given above (*Taxonomic notes*). Description based on eight Bornean larvae in pre-limb bud stages.

Body oval, slightly depressed, width of body about three-fifths of body length; eyes dorsal, not visible from below; spiracle sinistral, closer to eye than to end of body; anus dextral, opening at margin of ventral fin; tail muscle strong; fins beginning at root of tail; margins of both fins convex; dorsal fin deeper than ventral, deeper than caudal muscle in distal half; tip of tail rounded.

Mouth ventral, subterminal; beaks heavy, serrate, black; labial teeth I:5–5/4–4:I (2), I:5–5/5–5:I (3), or I:6–6/5–5:I (1) in larvae 14.5–18.0 mm. head-plus-body, I:4–4/3–3:I in a 6.0 mm. tadpole.

Color (in life) pale yellowish; an irregular mid-dorsal stripe of gold chromatophores in smaller larvae (i.e., body less than 10 mm.); patches of gold chromatophores laterally; a black interorbital band and a broader black band across root of tail; tail with widely scattered dark spots. Golden mid-dorsal stripe and caudal spots not visible in preserved specimens.

Ecological notes.—Adults were found in almost equal numbers in swamp forest (7) and well-drained hill forest (9). At night frogs were seen on forest floor (17), along the banks of small streams (4), or in seepage areas (3). Only two were caught by day and both were under dead wood on the forest floor.

The larvae described above were found in pools of small streams 0.5–3 m. wide or in temporary pools formed by receding flood waters.

The two known Bornean localities are within 300 m. of sea level.

Geographic variation.—See *Taxonomic notes* above.

Range.—Malay Peninsula, Singapore Island, and Borneo.

SARAWAK: Fourth Division, Nyabau, Sungei Pesu.

Megophrys Kuhl

Megophrys monticola Kuhl and van Hasselt

Material examined.—Borneo 71+7 lots of larvae (15+6 series of larvae FMNH; 10 MCZ; 2 MHNP; 7 NMB; 9 NHMW; 12 RMNH; 9+larvae SM; 3 UMMZ; 3 USNM; 1 ZMA); Sumatra 64 (1 NMB; 38 NHMW; 8 RMNH; 2 SNG; 14 ZMA; 1 ZMB); Singapore 6

TABLE 5.—Geographic variation in *Megophrys monticola*. Medians (means, in the case of snout-vent) in parentheses.

Subspecies	Area	Skin folds on body[1]	Upper eyelid[2]	Rostral projection[2]	Dorsal calcified skin[3]	Snout-vent lengths (mm.)[4]	
						Females	Males
m. nasuta	Borneo	2, long	110–210(153) N=20	25–65 N=16	533–755(597) N=9	89–121(110.0) N=11	70–104(86.5) N=8
m. nasuta	E. Sumatra	2, long	122–212(163) N=14	38–89 N=14	535–830(638) N=4	93–120(112.1) N=5	70–73 N=2
m. nasuta	Singapore	2, long	160–189(171) N=6	0–30 N=5	489–598(562) N=4	—	65–73(69.8) N=6
m. monticola	W. Sumatra	1, long	95–122(108) N=16	0 N=16	353–444(394) N=10	78–90(82.3) N=8	48–56(51.4) N=5
m. monticola	Java	1, long	—	0–30	—	75–95(83.5) N=6	44 N=1
m. stejnegeri	Mindanao	1, long	100–158(130) N=8	0–20 N=18	262–516(403) N=3	57–78(68.7) N=8	40–53(46.3) N=9
m. ligayae	Palawan	2, short	100–140(125) N=4	0 N=4	351 N=1	90 N=1	60–69(64.3) N=3

[1] Long, reaching almost to groin; short, extending only half of body length.
[2] In terms of thousandths of snout-vent.
[3] Length of calcified area in terms of thousandths of snout-vent; only frogs between 70 and 100 mm. used.
[4] Only females with enlarged ova, males with vocal sacs.

(FMNH); Malaya 2 (1 NHMW; 1 ZMB); Java 20 (7 AMNH; 13 USNM); Mindanao 14 (FMNH); Palawan 4 (FMNH).

Taxonomic notes.—The conspecific relationship between *monticola* and *nasuta* (Inger, 1954A) is borne out by examination of additional specimens from many parts of the range.

Individual variation in the length of the rostral appendage is shown not only in the Kina Balu sample (ibid.) but also in a series of six males from Bukit Timah, Singapore (FMNH 100917-22). In one of these males the appendage is absent, in one it is less than 0.5 mm., in another 0.5 mm., in another 1.8, and in another 2.3; the snout of the sixth is damaged but appears to have no appendage. The rostral appendage is uniformly absent in specimens from Padang, western Sumatra and 3–10 mm. long in those from eastern Sumatra.

To the characters previously used (ibid.) to differentiate among subspecies of *monticola*—i.e., number and length of skin folds on body, length of dermal "horn" over the eye, and presence or absence of vomerine teeth—may be added snout-vent length and the proportion of the dorsal skin that is calcified (Table 5).

Two subspecies occur in Sumatra. Of 38 specimens from Padang (RMNH 2144, NHMW 6589–90, 6596–8, 6601–03) on the mountainous western coast, all but one have the characteristics of *m. monticola*: one pair of skin folds, a short orbital "horn," and small size. Fifteen (NMB 2286, ZMA 5185–87) from eastern Sumatra have the long orbital projections, two pairs of skin folds, and large size of *m. nasuta*. The exceptional Padang frog (RMNH 2144) has the size (130 mm.) and dermal projections of *m. nasuta* but only one skin fold as in *m. monticola*. Two frogs (RMNH, unnumbered) from Rimbo Pengadang, 350 kilometers southeast of Padang, represent an intergrading population. The larger (a female, 73.1 mm.) has all the characteristics of *m. monticola*; the smaller (a juvenile 57.5 mm.) has the long rostral and orbital projections of *m. nasuta* and two skin folds on the right side, but only one fold on the left side, as in *m. monticola*.

Megophrys monticola nasuta (Schlegel). Figure 11.

Ceratophryne nasuta Schlegel, 1858, Handl. Dierk., **2**, p. 57, pl. 4, fig. 72—Sumatra.

Megalophrys nasuta Günther, 1873, Ann. Mag. Nat. Hist., (4), **11**, p. 419; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 443; 1892, Proc. Zool. Soc. London, **1892**, p. 508; 1908, *ibid.*, **1908**, p. 413, pl. 22; 1912, Fauna Malay Penin., Rept. and Batr., p. 279, fig. 77; Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 163; Bartlett, 1895, Sarawak Note Book,

no. 1, p. 14; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 10; Andersson, 1923, Meddel. Zool. Mus. Kristiania, no. 7, p. 121.

Megophrys nasuta Smith, 1930, Bull. Raffles Mus., no. 3, p. 132; 1931, *ibid.*, no. 5, p. 9; Brongersma, 1937, Zool. Meded., **20**, p. 7.

Megophrys monticola nasuta Inger, 1954, Fieldiana, Zool., **33**, p. 223, fig. 37B; 1954, Jour. Washington Acad. Sci., **44**, p. 250; 1956, Fieldiana, Zool., **34**, p. 393.

Pelobatrachus nasutus Beddard, 1907, Proc. Zool. Soc. London, **1907**, p. 909.

Megalophrys montana (part) Boulenger, 1908, *op. cit.*, p. 411; van Kampen, *op. cit.*, p. 10.

Megophrys monticola (not of Kuhl and van Hesselt) Smith, 1931, *op. cit.*, p. 12.

Material examined.—Listed above under *Megophrys monticola.*

Description.—A large species, adult males to more than 100 mm., females to more than 120 mm.; head and body stout; hind limbs feeble; head wider than long, width 0.43–0.50 of snout-vent (median 0.472; N=21) in Bornean adults; snout (fig. 8G) obtusely pointed, projecting beyond mouth, usually a conspicuous, dermal, rostral appendage; snout (without dermal appendage) subequal to eye diameter; upper eyelid drawn out into a long, triangular projection; width of eyelid (including projection) 0.10–0.21 of snout-vent; canthus rostralis sharp; lores almost vertical, concave; tympanum present, usually hidden by skin; vomerine teeth in two well-separated, rounded groups between or slightly behind choanae.

Tips of fingers blunt; first finger longer than second, second and fourth subequal; a large oval, inner palmar tubercle covering first metacarpal; subarticular tubercles not visible. Tips of toes like those of fingers; third toe longer than fifth; toes webbed at bases; third and fifth toes with 2⅔–3 phalanges and fourth with four phalanges free of web; inner metatarsal tubercle low, oval, as long as first toe; no outer metatarsal tubercle; no subarticular tubercles; tibia 0.34–0.42 of snout-vent (median 0.369; N=21) in Bornean adults.

Skin with two pairs of parallel, longitudinal folds, inner from occiput to groin, outer from rear of eye to groin; rarely a spur from outer skin fold to rictus; usually a large black tubercle on each side above shoulder between the two dermal folds; more rarely one or two tubercles in center of back; skin of head fused to skull, usually free in specimens smaller than 70 mm.; skin behind head calcified for varying distances; area of calcified skin (including that of head) covering 0.50–0.83 of snout-vent length; a small, conical pectoral gland mesad from arm insertion; skin laterally and ventrally rugose or coarsely granular.

FIG. 11. *Megophrys monticola nasuta.*

Color in life pale or dark brown above; in alcohol paler; a large dark area usually occupying median strip of back and sending wide branches to upper eyelid; a black bar below and somewhat behind eye; often a dark streak below canthus; usually no temporal dark area; limbs above with narrow, dark crossbars; ventrally grayish or brownish; throat usually solid brownish black in males, with a longitudinal, dark median stripe in females.

Secondary sex characters.—Despite extensive overlap, adult females are significantly larger than males (Table 5). Males have relatively longer legs, the tibia length (in thousandths) of snout-vent being 361–423 (median 397) in males and 341–405 (median 359) in females; the difference between the two sets of ratios is statistically significant (P=0.002), applying the Mann-Whitney U test. The

sexes do not differ in relative head width (males: 433–495, median 466; females: 451–495, median 472).

Males have median subgular vocal sacs having a small round opening on each side of the mouth (Liu, 1935; Inger, 1954A). The dark brown nuptial pads cover the dorsal and median surfaces of the distal half of the metacarpal and the proximal half of the basal phalanx of the first finger and usually a narrow dorsomedial strip of the second.

Larvae.—Seven lots of Bornean tadpoles having funnel mouths belong to this species. Developmental stages range from pre-limb bud to metamorphosis. The most advanced larva has erupted forelimbs, no larval lips, the gape of the mouth not extending beyond a perpendicular from the nostril, two lines marking the site of the skin folds of the body, and a light thickened spot at the center of the margin of the eyelid marking the future orbital projection.

Body ellipsoidal, about twice as long as broad, flattened above; eyes dorsolateral, barely visible from below; spiracle sinistral, much closer to eye than to end of body; anus median, anal tube separated from ventral fin; tail muscle strong; fins beginning at root of tail, margins subparallel; dorsal fin deeper than caudal muscle only in distal fourth; ventral fin not as deep as dorsal; tail tapering gradually from center to blunt point.

Mouth terminal, with funnel-shaped lips; lips without papillae; beaks weak, serrated.

Color (in alcohol) dark brown above, with or without obscure black spots; below body pale, usually with small black spots especially ventrolaterally; caudal muscle brown, a few small, black spots; upper fin dusky with light spots near tip; lower fin colorless except for dark network in distal quarter.

Six tadpoles in pre-limb bud stage have head-plus-body lengths of 8.9–11.6 (mean 9.9) and total lengths of 28.0–34.0 mm. Head-plus-body lengths in two Stage XIX larvae are 12.6 and 13.1 mm.; their total lengths are 41.0 and 39.0 m., respectively.

Ecological notes.—*Megophrys monticola nasuta* is a characteristic member of the forest floor fauna. The cryptic qualities of its coloration and form when the frog remains still among dead leaves (fig. 11) have been commented on often (e.g., Boulenger, 1912). The excellent camouflage makes this species difficult to locate by day; our field parties were able to collect only three during daylight hours—two juveniles under dead leaves and one subadult on the forest floor. At

night, reflected light from the frog's large eyes makes collecting easier, and we caught five adults on stream banks and two on the forest floor well away from water.

Larvae are found in the slow, ponded portions of small streams usually where dead leaves have accumulated on the silty bottom, or in small, semi-isolated pools having similar bottoms alongside such streams. Presumably the plankton on which the larvae feed (Boschma, 1922; Smith, 1926) are more abundant in these situations than where the current is stronger.

The Bornean specimens I examined have the following altitudinal distribution:

Meters	0–100	100–200	201–500	501–1000	1001–1500	1501—
Adults	5	10	4	18	9	1
Larval series	4	2	0	0	0	0

One specimen (FMNH 77311) was caught on the sea beach at Santubong, Sarawak. The maximum elevation is 1675 meters (Lumu Lumu: MCZ 22637). This frog apparently lives equally well at all elevations below 2000 meters in Borneo. Somewhat higher elevations are reached in Sumatra and Java (fig. 12). Its scarcity below 800 meters in Java (Mertens, 1934) may be caused by extensive modification of the environment by man.

Geographic variation.—The only local differentiation observed in the Bornean sample involved the dermal appendages of the head

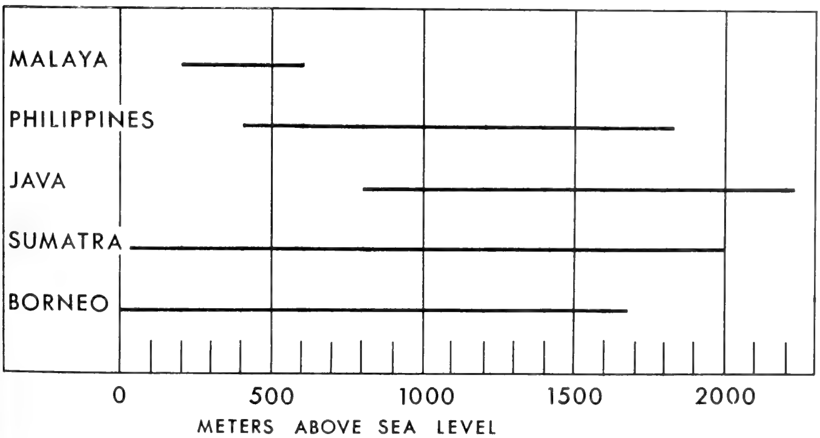


FIG. 12. Altitudinal distribution of *Megophrys monticola*. Data for Malaya from Flower (1896, 1899); for Philippine Islands from Inger (1954A); for lowest Javan elevation and for highest Sumatran elevation from Mertens (1934).

(Table 6). Frogs from the Kina Balu area have smaller projections than those from other parts of Borneo.

Range.—Southern half of the Malay Peninsula (Smith, 1930), Sumatra, and Borneo (fig. 13).

TABLE 6.—Geographic variation in dermal appendages (in terms of thousandths of snout-vent) of Bornean *Megophrys monticola nasuta*.

Area	Map no.[1]	N	Eyelid[2]	Rostral appendage
Kina Balu	1	3	110–128	25–31
Sarawak	2	3	140–162	34–52
Central Borneo	3	5	159–175	48–64
Southeastern Borneo	4	3	150–160	33–64

[1] Numbered areas in fig. 13.
[2] Width of eyelid plus dermal projection.

SABAH: Kota Belud District, Kiau, Lumu Lumu, Marei Parei (Smith, 1931A); Ranau District, Bundu Tuhan, Sungei Kepungit, Sungei Mamut, Sungei Matukungan; Sandakan District, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tawau District, Kalabakan. SARAWAK: First Division, Buso, Kuching, Matang, Paku, Santubong, Tegora; Third Division, Baleh River valley near mouth of Putai River, Mengiong River; Fourth Division, Mount Dulit (Bartlett, 1895), Long Sinei, Niah. KALIMANTAN: Sungei Bluu, Bulungan (Andersson, 1923), Kahajan River, Gunong Kenepai, Liang Kubung, Long Petah, upper Mahakam valley, Muara Teweh, Nunukan Island.

Megophrys baluensis (Boulenger)

Leptobrachium baluense Boulenger, 1899, Ann. Mag. Nat. Hist., (7), **4**, p. 453—Mount Kina Balu, Sabah.

Megalophrys baluensis Boulenger, 1908, Proc. Zool. Soc. London, **1908**, p. 429; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 16.

Megophrys baluensis Smith, 1931, Bull. Raffles Mus., no. 5, p. 30; Inger, 1954, Jour. Washington Acad. Sci., **44**, p. 250.

Material examined.—Borneo 14 (5 BM, including holotype; 4 FMNH; 3 MCZ; 2 USNM).

Description.—A moderate-sized *Megophrys*, males 40–45 mm., females 55–70 mm.; head and body stout; hind limbs short; head wider than long, width 0.41–0.48 of snout-vent (median 0.434; N = 9); snout extremely short (fig. 8H), broadly rounded, vertical in profile; no rostral appendage; upper eyelid with a short, narrow projection from lateral margin (fig. 8H) and usually an erect, conical tubercle dor-

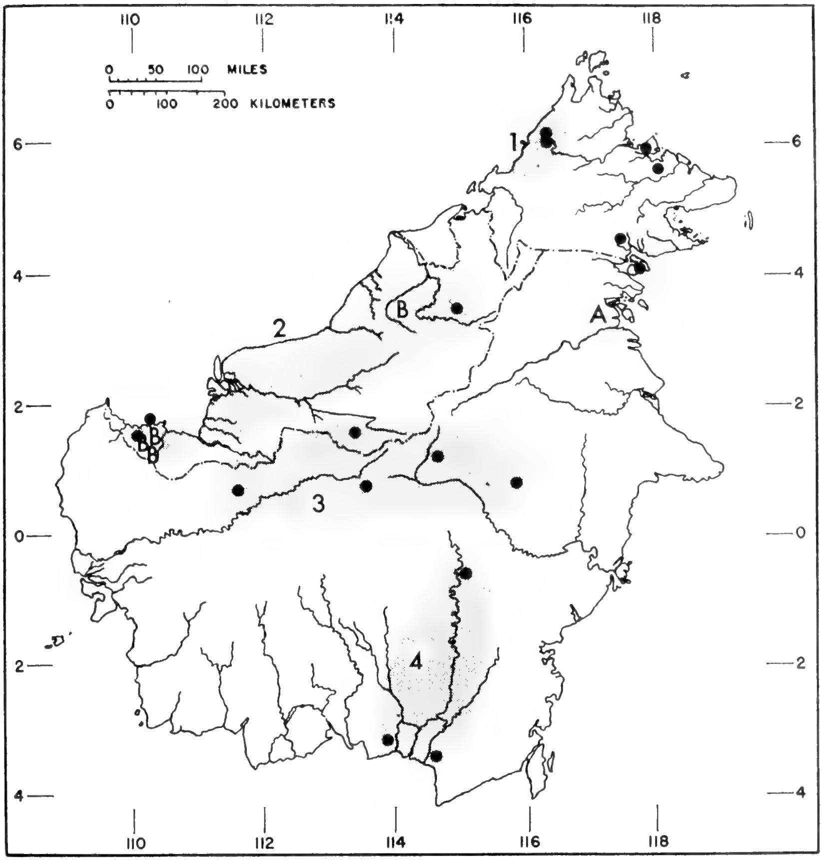


FIG. 13. Known localities of *Megophrys monticola nasuta* on Borneo. Specimens examined from places marked with black circles. Species reported by Bartlett (1895) from areas marked B, by Andersson (1923) from area marked A. Numbers explained in Table 6.

sally; canthus rostralis sharp; interorbital much wider than upper eyelid (without dermal appendage); lores vertical, weakly concave; tympanum present, usually visible through skin, less than half diameter of eye, separated from eye by at least twice its diameter; vomerine teeth in two well-separated, rounded groups slightly behind level of choanae.

Tips of fingers blunt; first finger shorter than second; second and fourth subequal; an oval inner palmar tubercle covering first metacarpal; subarticular tubercles not visible. Tips of toes like those of fingers; third toe longer than fifth; toes without web or with rudi-

mentary web at bases; third and fifth toes with three phalanges and fourth with four phalanges free; inner metatarsal tubercle low, oval, almost as long as inner toe; no outer metatarsal tubercle; no subarticular tubercles or with weak basal ones only; tibia 0.36–0.44 of snout vent (median 0.400, N = 8).

Skin above with oval or ridge-like tubercles arranged roughly in a dorsolateral and a lateral row; no continuous longitudinal folds; an angulate supratympanic fold from eye to axilla; osteoderms in cephalic skin, but skin not fused to skull; no calcification in skin behind head; a conical pectoral gland mesad from axilla; skin rugose or coarsely granular laterally and ventrally behind chest.

Color (in alcohol) dark brown above, pale yellowish laterally, the dark area usually ending abruptly at the dorsolateral line; top of head anterior to eyes lighter than back; an obscure dark triangle usually present, corners on eyelids and occiput; a dark bar from below center of eye to lip followed by narrow, oblique, light bar and a broad dark band covering entire temporal region; limbs with narrow dark crossbars dorsally; below yellow or whitish with brown spots or mottling especially heavy on throat; throat with a dark, median, longitudinal streak.

Secondary sex characters.—Seven females containing enlarged ova measure 56.0–69.6 mm. (mean 64.16); the two adult males seen measure 40.9 and 45.0 mm.

A weak, yellowish nuptial pad covers the dorsal and median surfaces of the distal half of the metacarpal and proximal half of the basal phalanx on the first finger and a small circular area on the dorsal surface above the end of the second metacarpal. The vocal sac has small round openings near the commissures of the jaws.

Ecological notes.—The three specimens for which I have detailed information were collected at night in primary rain forest, one of them on the bank of a stream and two on the forest floor at some distance from water. These three frogs were found at elevations between 100 and 300 meters above sea level. The species has been collected on Mount Kina Balu at elevations between 1280 and 1675 meters above sea level. On that mountain the tall forest extends up to 1800 meters in sheltered valleys and mossy, montane forest down to 1500 meters on exposed ridges (Chasen *in* Smith, 1931A).

Range.—Borneo.

SABAH: Kota Belud District, Lumu Lumu; Ranau District, Bundu Tuhan. SARAWAK: Third Division, Mengiong River.

Nesobia van Kampen

Nesobia mjobergi Smith

Leptobrachella mjobergi Smith, 1925, Sarawak Mus. Jour., **3**, p. 28, figs. A–D—Mount Gadin, Sarawak.

Leptobrachella baluensis Smith, 1931, Bull. Raffles Mus., no. 5, p. 12, pl. 1, fig. 4—Kamboranga, Mount Kina Balu, Sabah.

Material examined.—Borneo 45 (4 BM, including holotypes of *mjobergi* and *baluensis*; 36 FMNH; 2 RMNH; 3 SM).

Taxonomic notes.—Smith (1931A) distinguished between the two nominal forms on the basis of tongue shape ("feebly nicked" in *mjobergi*, "not nicked" in *baluensis*) and the relative lengths of the second and fourth fingers (equal in *mjobergi*, second longer in *baluensis*). According to my observations, the two fingers are equal in the holotype of *baluensis* and in almost all of the specimens examined. In a series of 23 frogs from Deramakot, Sabah, about one-half have a weak notch at the rear of the tongue and the rest have smooth-margined tongues. Variation of this sort prohibits use of tongue shape as a criterion for specific differentiation in this group.

Nesobia mjobergi does show geographic variation (see below p. 52) in Borneo, but that variation does not seem to be great enough to warrant recognition of distinct forms. The habitat and behavior are apparently uniform throughout the range.

The Bornean species can be distinguished from *N. natunae* by the absence of a dark temporal blotch and by the presence of a dark interorbital bar.

Description.—A small pelobatid, males 15–19 mm., females to about 23 mm.; habitus moderately stocky to slender; limbs slender; head almost as broad as long, width 0.30–0.37 of snout-vent; snout obtusely pointed, rounded or slightly projecting in profile; nostril slightly closer to tip of snout than to eye; canthus distinct, rounded; lores oblique, weakly concave; diameter of eye shorter than snout; interorbital wider than upper eyelid, greater than eye-nostril distance; tympanum distinct, its diameter slightly less than half that of eye, greater than its distance from eye; no vomerine teeth; maxillary teeth present.

Tips of fingers slightly dilated, sharply pointed, skin of ventral surface of disk distinct from skin of remainder of fingers; first finger shorter than second; subarticular tubercles weak; a large, raised, inner palmar tubercle, not extending out along first metacarpal; a palmar sesamoid ossicle. Tips of toes (fig. 8A) like those of fingers but

slightly larger; third toe longer than fifth; rudimentary web at bases of toes, four phalanges of fourth toe free; subarticular tubercles obscure; a long, low, inner metatarsal tubercle, no outer one; tibia 0.48–0.56 of snout-vent.

Skin above smooth or shagreened, a few small, round, scattered warts; a distinct supratympanic fold from eye to axilla; sides coarsely granular, venter smooth; a small, conical pectoral gland medial to axilla.

Color (in alcohol) gray or brown above, usually a dark interorbital bar and a suprascapular W-shaped mark; less often a dark, sacral, inverted V; pale dorso-lateral stripes evident in a few specimens; limbs with dark, dorsal crossbars; light spots on lips; venter whitish with pale dusting of melanophores or with a dark network.

Secondary sex characters.—Twenty-one males with vocal sacs measure 15.0–18.2 mm. (mean 15.98 ± 0.17). The three females seen measure 18.2–22.5 mm.

Males have median subgular vocal sacs having round openings far back in the mouth. Lineae masculinae are present in about half the males (see below).

Ecological notes.—The 34 specimens for which detailed habitat notes are available were caught along small, swift streams in primary rain forest. The frogs were on rocks projecting out of the water, on rocks at the edge of the streams, or on low vegetation (ca. 0.3–0.6 meters high) growing out of the rocky beds.

TABLE 7.—Comparison of male *Nesobia mjobergi* from two localities in Borneo. Ten frogs from each locality.

	Range	Median	U[1]	P
		Head width[2]		
Deramakot, Sabah	301–329	313	15.5	0.02
Matang, Sarawak	315–369	342		
		Tibia length[2]		
Deramakot	482–546	526	49.5	0.10
Matang	497–571	527		
	Range	Mean	t	P
		Snout-vent (mm.)		
Deramakot	15.0–16.6	15.60 ± 0.17	2.48	0.03
Matang	15.3–17.3	16.36 ± 0.26		

[1] U of Mann-Whitney test.

[2] In terms of thousandths of snout-vent.

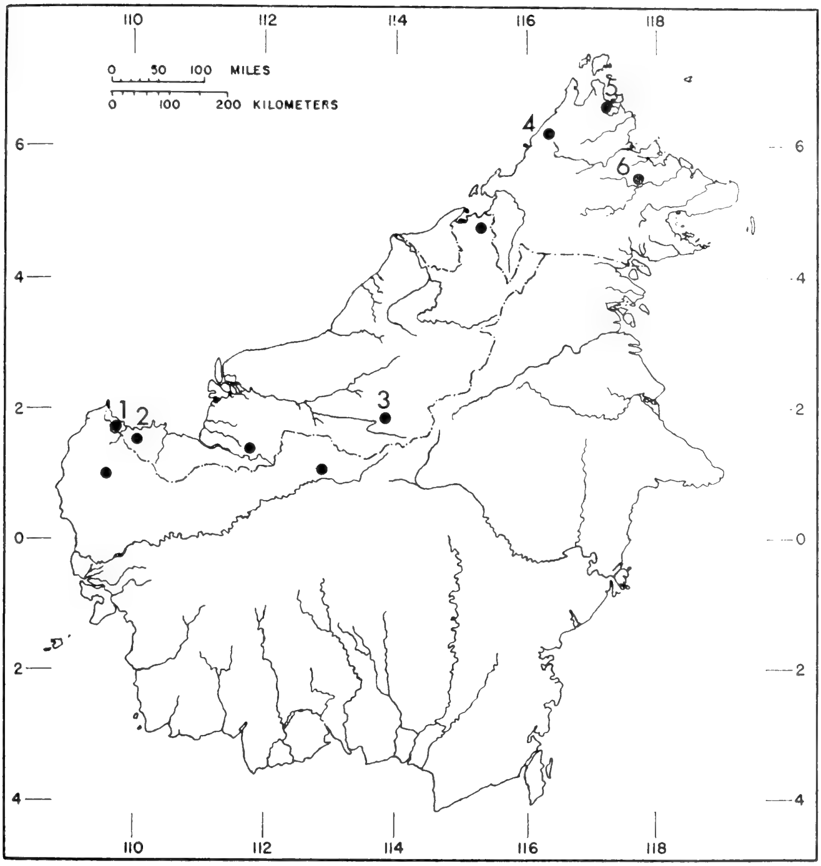


FIG. 14. Known localities of *Nesobia mjobergi*. Numbers explained in text.

Altitudinal range is extensive. All of the frogs mentioned above were caught within 200 meters of sea level. The holotype of *mjobergi* was caught at 609 meters (Smith, 1925B), the holotype of *baluensis* at 2200 meters (Smith, 1931A), and a specimen (RMNH unnumbered) from Kalimantan at 1200 meters.

Both large series consisted of males calling at night, one early in May and the other late in July. A gravid female (FMNH 76600) was caught just a few inches from a calling male on a rock in the middle of a shallow riffle. The presence of that female and the association of all calling males with riffles indicate that oviposition takes place in swift water and, possibly, under rocks. That possibility is sug-

gested by the absence of pigment in the ovulated eggs of the gravid female. Other pelobatids (e.g., *Oreolalax* and *Scutiger*) are known to oviposit under rocks (Liu, 1950).

Geographic variation.—Two series, one from Matang (locality numbered 2 in fig. 14) in southwestern Sarawak and one from Deramakot (locality numbered 6 in fig. 14) in eastern Sabah, differ slightly but not in the characters Smith (1931A) mentioned. The frogs from Matang (FMNH 77199–77209) have pale venters with a light dusting of melanophores uniformly distributed, whereas those from Deramakot have a dark network ventrally. The holotype of *mjobergi* from Mount Gadin (locality 1) resembles the frogs from nearby Matang in this character; the holotype of *baluensis* (from locality 4) is like the Deramakot frogs. All but one of the 11 males from Matang have pink lineae masculinae, whereas only one of 10 from Deramakot does.

The two sets of males differ slightly but significantly in snout-vent length and in relative head width, but not in tibia length (Table 7). The holotype of *baluensis* has a head-width ratio of 0.331, hence in the range of the Matang series. I failed to measure the head width of the holotype of *mjobergi*.

A mature male from the middle Baleh valley (locality number 3 in fig. 14) is larger (18.2 mm.) than those from Matang or Deramakot. It resembles the Deramakot males in having a dark network ventrally and in lacking lineae masculinae, but is like the Matang series in head width (0.335).

Range.—Borneo (fig. 14).

SABAH: Kinabatangan District, Kota Belud District, Kamboranga; Kudat District, Paitan Bay. SARAWAK: First Division, Mount Gadin, Matang, Mount Poi; Second Division, Lupar River valley; Third Division, Baleh River near mouth of Putai River, Mengiong River; Fifth Division, Lawas. KALIMANTAN: Mount Damus near Sambas, Mount Tibang.

BUFONIDAE

The Indo-Malayan fauna includes six genera of bufonids, five of which represent different modes of life. Information is lacking on the natural history of the sixth, *Cacophryne*. All six genera occur in Borneo.

Bufo, the only one of these genera occurring outside the Oriental tropics, typically is a warty, stocky, terrestrial amphibian. Its numerous, small, pigmented ova are laid in standing or slowly moving water and its larvae are generalized, having spheroidal bodies, rather narrow lips, horny beaks, highly coiled intestines, and deep fins.

Pedostibes is distinguished from *Bufo* by its expanded digit tips and its arboreal habits. The ova and tadpoles are like those of *Bufo*. Breeding takes place in small forest streams.

Pseudobufo, a monotypic genus, is an aquatic toad having somewhat depressed habitus, long slender fingers, completely webbed feet, dorsal nostrils, reduced ossification (Tihen, 1960), and no parotoid glands. The ova are small, numerous, and pigmented. As the habitat is standing or very slowly moving water, probably the tadpoles resemble the nonspecialized ones of *Bufo*.

Ansonia, slender-bodied and long-legged, is terrestrial but breeds in riffles or cascades in forest streams. The tips of the digits are usually expanded and the webbing of the toes is membranous rather than thick as in *Bufo*. Though the adults differ from *Bufo* morphologically (Inger, 1960B), *Ansonia* is most sharply differentiated from *Bufo* in its reproductive habits and larval life. The ova are relatively large, few in number, and non-pigmented (Inger, 1954A) and are undoubtedly laid in relatively swift water (perhaps under rocks). The larvae have typical torrent-adapted forms: the lips are expanded to form oral suckers, the body is streamlined, and the fins low (Inger, 1960B).

Pelophryne is terrestrial and probably partly arboreal. The fingers and toes have a peculiar, fleshy web, the coccyx is fused to the sacral vertebra and has a dorsal flange, and the number of presacral vertebrae is reduced from eight to seven. The axial skeleton suggests that *Pelophryne* creeps rather than hops. The reproductive

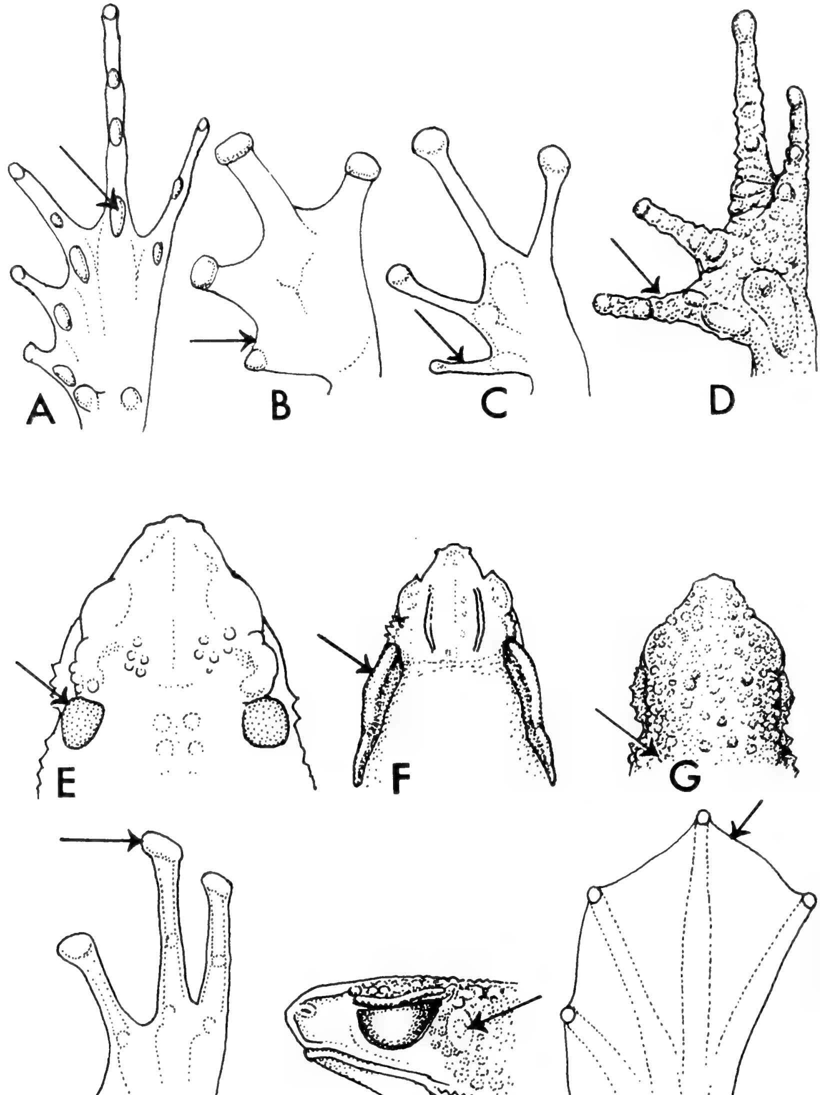


FIG. 15. Key to Bornean Bufonidae.

pattern is greatly modified: the ova are very large (see below), the clutch size is less than 20, and the ova are laid in small rain-filled depressions. The only known larvae have vestigial mouth parts, very feebly coiled intestines, and probably subsist entirely on yolk (Inger, 1960A).

KEY TO GENERA OF BUFONIDAE OCCURRING IN BORNEO (Fig. 15).

1A. Underside of foot with a large, elongate tubercle near base of each toe (fig. 15A) *Cacophryne.*
B. Underside of foot various but never as in 1A .... 2.

2A. At most one phalanx of first finger projecting from fleshy web (fig. 15B); adults never exceed 40 mm. .... *Pelophryne.*
B. Two phalanges of first finger projecting free of palm or web (fig. 15C, D); hands without fleshy web .... 3.

3A. Distinct parotoid gland behind eye (fig. 15E, F) .... 4.
B. No parotoid gland (fig. 15G) .... 5.

4A. Tips of fingers rounded, not dilated (fig. 15D) .... *Bufo.*
B. Tips of fingers dilated into truncate disks (H) .... *Pedostibes* (part).

5A. Fourth toe broadly webbed to tip (fig. 15I) .... *Pseudobufo.*
B. Fourth toe not broadly webbed to tip .... 6.

6A. No tympanum .... *Pedostibes* (part).
B. Tympanum visible (fig. 15J) .... *Ansonia.*

KEY TO KNOWN TADPOLES OF BORNEAN BUFONIDAE

1A. Papillae continuous across lower lip; upper beak divided .... 2.
B. Papillae confined to lateral corners of lower lip; upper beak in one piece .... 4.

2A. Gap between halves of upper beak smaller than length of one half. . *Ansonia* sp.
B. Gap between halves of upper beak at least equal to length of one half ...... 3.

3A. A single, marginal row of papillae across width of lower lip *Ansonia albomaculata.*
B. A marginal and an inframarginal row of papillae across width of lower lip *Ansonia minuta.*

4A. All labial tooth rows uninterrupted, two rows on upper lip and three on lower *Bufo biporcatus.*
B. Inner row of teeth on upper lip interrupted *Bufo melanostictus* and *Pedostibes hosei.*

Tadpoles of the last two species are very similar in general form and in the usual characters by which species of tadpoles are distinguished. For the purpose of rapid identification, which is after all the only function of these artificial keys, these two kinds of larvae can be recognized on ecological grounds. *Bufo melanostictus* does not occur in forest, *Pedostibes hosei* does; *B. melanostictus* occurs in towns,

P. hosei does not (pp. 73 and 96). In general the tadpole of *B. melanostictus* is larger and darker than that of *P. hosei*, but these differences are apparent only when specimens of both are available.

Bufo Laurenti

KEY TO BORNEAN SPECIES OF BUFO (Fig. 16).

1A. A pair of crests between eyes running back on to parietal region (fig. 16A) . . 2.
B. If crests present between eyes, they do not continue back on to parietal region (fig. 16B) . . . . 3.

2A. Parotoid long, narrow, and sharply raised; its maximum width at most one-fifth its length (fig. 16C) . . . . *quadriporcatus*.
B. Parotoid triangular or oval, its maximum width at least two-fifths its length (fig 16D) . . . . *biporcatus divergens*

3A. At least one phalanx of third and fifth toes free of web (fig. 16E) . . *melanostictus*.
B. Only tips of third and fifth toes free of web (fig. 16F) . . . . 4.

4A. Parotoid gland about twice as long as wide (fig. 16G) . . . . *juxtasper*.
B. Parotoid gland round or triangular, never twice as long as wide (fig. 16H) *asper*.

Bufo biporcatus Gravenhorst

Material examined.—Java 14 (3 AMNH; 2 BM; 3 FMNH; 1 USNM; 5 ZMB); Bali 5 (1 AMNH; 3 FMNH; 1 ZMB); Borneo and Sumatra (see under *biporcatus divergens*); Philippine Islands 89 (FMNH); Malaya 3 and Thailand 1 (*parvus*—FMNH).

TABLE 8.—Geographic variation in *Bufo biporcatus*.

	Males			Females		
	Snout-vent (mm.)					
	No.	Range	Mean	No.	Range	Mean
Java[1]	57	37–53	48.3±0.43	17	47–68	58.7±1.52
Borneo	32	28.5–42.7	36.72±0.52	16	40.3–52.0	46.15±0.87
Palawan	20	52.0–64.5	57.84±0.74	20	58.3–75.5	66.38±1.05
Busuanga	12	62.9–77.8	70.39±1.13	5	69.3–89.5	80.32±3.11
	Tibia[2]					
	No.	Range	Median	No.	Range	Median
Java	5	341–376	374	7	334–375	351
Borneo	13	360–477	442	14	316–453	433
Palawan	12	364–434	410	12	353–417	390
Busuanga	12	378–428	408	5	358–402	361
	H[3]=22.20		P <0.001	H=12.00		P=0.01

[1] Data from Church (1960).
[2] In terms of thousandths of snout-vent.
[3] From Kruskal-Wallis test (Siegel, 1956).

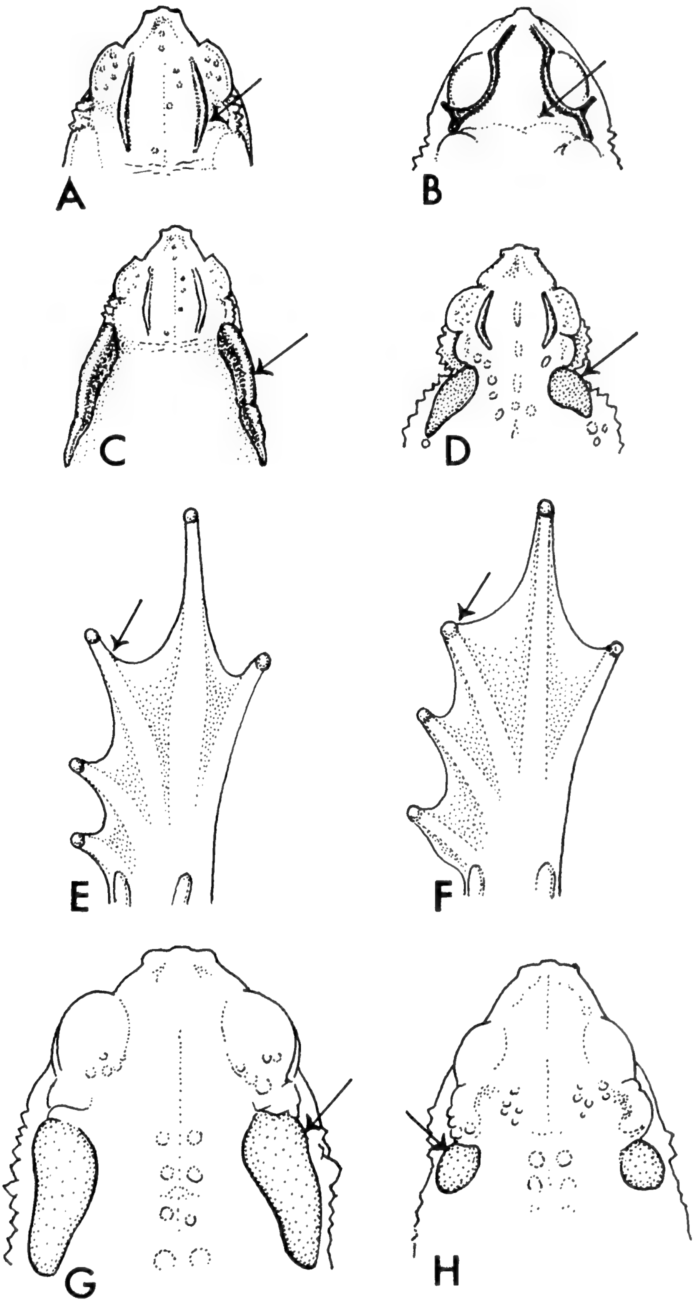


FIG. 16. Key to Bornean species of *Bufo*.

Taxonomic notes.—Though very similar to Javanese and Balinese specimens, Bornean toads differ from them in size and relative length of leg (Table 8).

The snout in Javan *biporcatus* is much narrower at the top than at the mouth so that the lores are conspicuously sloping. The narrowest portion of the upper surface of the snout in these specimens is narrower than either the diameter of the tympanum or the space between the supraorbital ridges at their origins. In contrast, the snout of Bornean *biporcatus* is almost as wide dorsally as ventrally so that the lores are vertical or nearly so. The dorsal surface of the snout in the Bornean toads is as wide at its narrowest point as the tympanum and as wide as the space between the supraorbital ridges at their origins.

On the basis of these differences the Bornean population should be recognized as a distinct subspecies for which the name *divergens* Peters is available.

Differences between the Philippine form, *Bufo biporcatus philippinicus* Boulenger, and Bornean and Javanese toads in shape of parotoids, form of the supraorbital crests, and presence of an oblique row of lateral warts have been described (Inger, 1954A). As Table 8 shows, *B. b. philippinicus* also differs from the two other forms in size and relative leg length.

Four of the five Sumatran toads seen (AMNH 775; NMB 2288–90) have the characteristics of *b. divergens*, i.e., vertical lores, relatively long leg (tibia ratio 0.403–0.448), and small size (adult male 31.7, adult female 40.2, juvenile females 28.5 and 34.3 mm.). Three of these are from Palembang, eastern Sumatra, and the fourth lacks a definite locality. A fifth Sumatran specimen (ZMB 15493), from Gunung Raja in the southwestern corner of Sumatra, has sloping lores and short legs (tibia ratio 0.349) as in *b. biporcatus*; it is an immature female (41.5 mm.). Apparently, two subspecies occur in Sumatra. As in the case of *Megophrys monticola* (p. 41), the eastern lowlands of Sumatra have the form (*Bufo biporcatus divergens*) found in Borneo, whereas the western highlands have the form (B. *b. biporcatus*) found in Java.

Probably *Bufo parvus* Boulenger of the Malay Peninsula should be treated as a subspecies of *biporcatus*. Its supraorbital crests are like *biporcatus*, and its snout-vent length (3 adult males 32.5–37.6 mm., 1 adult female 38.6 mm.) and tibia ratio (0.428–0.446) agree with *biporcatus divergens*. It differs from *b. biporcatus* and *b. divergens* in having the parotoid uniformly oval (in the four studied) and

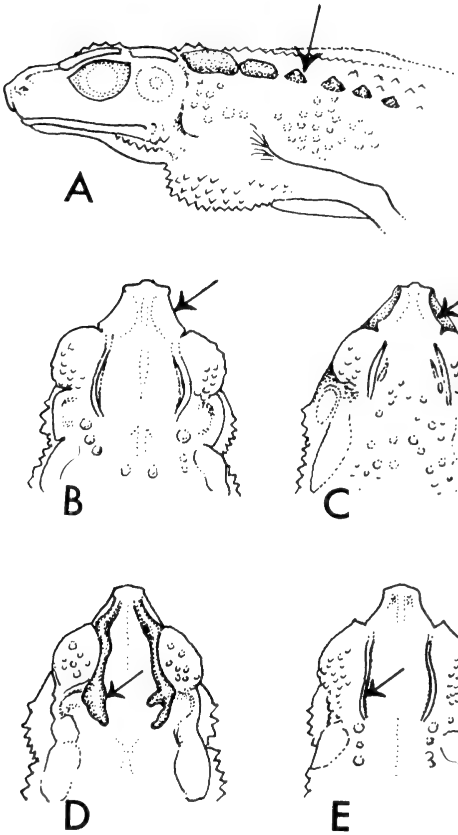


FIG. 17. Key to forms related to *Bufo biporcatus.*

in lacking the oblique, lateral row of conspicuous warts. I suspect that the specimens of *divergens* reported from Malaya (Boulenger, 1912) are *parvus.*

The forms allied to *Bufo biporcatus biporcatus* may be distinguished by use of the following key (fig. 17).

1A. Parotoid continuous with an oblique row of conspicuously enlarged warts (fig. 17A) . . . . 2.
B. Parotoid usually not followed by such warts . . . . 4.

2A. Parotoid long, narrow, and sharply raised; its maximum width rarely more than one-fifth its length (fig. 16C) . . . . *Bufo quadriporcatus.*
B. Parotoid triangular or oval, its maximum width at least two-fifths its length. 3.

3A. Lores vertical or nearly so (fig. 17B); dorsal surface of snout[1] at least as wide as tympanum.......... *Bufo biporcatus divergens.*
B. Lores distinctly sloping (fig. 17C); dorsal surface of snout[1] not as wide as tympanum.......... *Bufo biporcatus biporcatus.*

4A. Cranial crests distinctly thickened immediately behind level of eyes (fig. 17D) *Bifo biporcatus philippinicus.*
B. Cranial crests not thickened behind eyes (fig. 17G).......... *Bufo parvus.*

Bufo biporcatus divergens Peters

Bufo divergens Peters, 1871, Monatsber. Akad. Wiss. Berlin, **1871**, p. 579—Sarawak; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 312; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 88 (part); Smith, 1925, Sarawak Mus. Jour., **3**, p. 30.

Bufo biporcatus Boulenger, 1882, *op. cit.*, p. 311 (part); Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 158; van Kampen, 1905, Zool. Jahrb., (Syst.), **22**, p. 710; 1923, *op. cit.*, p. 90 (part); Smith, 1931, Bull. Raffles Mus., no. 5, p. 30.

Bufo biporcatus biporcatus Inger, 1954, Fieldiana, Zool., **33**, p. 228; 1956, *ibid.*, **34**, p. 394 (part).

Material examined.—Borneo 144 (12 BM; 93 FMNH; 4 MCG, including types of *divergens*; 2 MCZ; 5 MHNP; 5 NHMW; 1 NMB; 3 RMNH; 7 SM; 10 SNG; 1 USNM; 1 ZMA); Sumatra 5 (1 AMNH; 4 NMB); Great Natuna 2 (BM).

Description.—A small-sized *Bufo*, males to about 45 mm., females to 50–55 mm.; body stocky, limbs slender; head with a pair of continuous supraorbital-parietal crests, usually curved and diverging posteriorly; a short, thin supratympanic crest; head wider than long; snout truncate, usually with a small median bulge at the tip, projecting and oblique in profile, equal to or slightly longer than diameter of eye; nostril at tip of snout; canthus sharp; lores vertical or nearly so; interorbital wider than upper eyelid; tympanum distinct, about three-fifths diameter of eye.

Fingers moderately long, tips blunt, not swollen; first finger longer than second; subarticular tubercles conspicuous, simple; supernumerary metacarpal tubercles present. Tips of toes like those of fingers; fourth toe much longer than third and fifth; toes about one-half webbed; third and fifth toes with 1–1½ phalanges free, fourth with 3½–4 free of webbing; subarticular tubercles conspicuous, round, much smaller than metatarsal tubercles; inner metatarsal tubercles oval, shorter than first toe; a smaller, round outer metatarsal tubercle;

[1] Dorsal surface of snout measured at narrowest point behind nostrils.

no tarsal ridge, but a row of enlarged, spinose tubercles on inner edge of tarsus; tibia 0.32–0.48 of snout-vent (see Table 8).

Skin above and on sides with numerous, small, conical warts, those of sides usually slightly more elevated; warts in dorso-lateral region usually capped with 3–7 spinules (fig. 18B); ventrally coarsely granular; parotoid oval or, more often, triangular, separated from eyelid, length of parotoid 0.088–0.183 (median 0.126; N = 17) of snout-vent, parotoid width 0.35–0.80 (median 0.53; N = 17) of its length; an oblique row of enlarged, lateral warts follow parotoid.

Color (in life) usually clay brown or blackish brown above and on sides; a dark interorbital bar usually present; back with several isolated black spots or with several inverted black chevrons; a thin, light vertebral line present or absent; limbs with dark crossbars; below yellow or pale brown, immaculate or with dark mottling on throat and chest.

Secondary sex characters.—Females average about 10 mm. larger than males (Table 8). The sexes do not differ significantly in relative tibia length (Table 8) or tympanic diameter (males 0.049–0.069, median 0.064; females 0.051–0.069, median 0.059).

Males have median subgular vocal sacs with one or two slit-like openings (Liu, 1935; Inger, 1954A). Only one out of 20 Bornean males examined for this character had vocal sac openings on both sides of the mouth.

The nuptial pad consists of a blackish cluster of minute spines covering the dorsal and medial surfaces of the first finger from the base of the finger to the end of the basal phalanx. In 16 of 34 Bornean males, a small oval cluster of the nuptial spinules appeared on the medial edge of the second finger. Lineae masculinae are not present in Bornean males.

Larvae.—Van Kampen (1910B) and Schijfsma (1932) assigned larvae to *biporcatus* without providing a detailed description or direct evidence of relationship to adults. The evidence adduced by van Kampen consisted of similarity of tadpoles to those of *B. melanostictus* and the absence of adult *melanostictus* from the areas of collection, Lombok and Celebes.

Van Kampen (1910B, 1923) limited his descriptions of *biporcatus* larvae to the comments that they resembled those of *melanostictus* except for differences in the lengths of the two outer tooth rows of the lower lip. Subsequent references to *biporcatus* larvae (e.g., Bourret, 1941, p. 181) have merely paraphrased van Kampen.

Eggs were laid and fertilized in a plastic bag by a pair of *Bufo biporcatus divergens* (FMNH 138858–59) from Borneo. Larvae hatching from these eggs were reared until the oral apparatus had developed and active feeding had begun. We collected seven additional series of larvae matching those from known parents and including all stages of development from prior to the appearance of limb buds to metamorphic stages.

These larvae resemble those assigned to *Bufo parvus* by Smith (1916A, 1930). They differ from larval *B. melanostictus* described by van Kampen (1927) in having all rows of labial teeth uninterrupted.

The following description is based on numerous Bornean larvae.

Head and body oval, slightly flattened below; eyes dorsal, diameter of eye three-fourths to equal to interorbital width, greater than eye-nostril distance; interorbital about three-fourths length of snout: nostrils much closer to eye than to tip of snout; oral disk ventral, subterminal, about one-third maximum body width; papillae short, in a single row confined to corners of mouth; labial teeth II/III (28 counted); rows of upper lip equal, longer than rows of lower lip, which are subequal; beaks smooth, narrowly edged with black; spiracle sinistral, just below line connecting center of eye and root of hind limb, closer to hind limb than to eye; tail lanceolate, tip rounded; dorsal fin slightly deeper than ventral one; fins deeper than caudal muscle in distal half of tail; dorsal fin beginning over posterior fourth of body.

Color of body dark gray or brown above, whitish below; caudal muscle gray, lighter below; dorsal fin gray, with melanophores dense; ventral fin with band of melanophores along its base.

Total length 12.4 mm. in Stage III (stage 28 of Limbaugh and Volpe, 1957) tadpole; 17.1 to 17.8 mm. in Stages IX to XX; tail length equals 0.57–0.67 of total length.

One set (FMNH 151522–27) of larvae was reared to early metamorphic stages. When collected on November 8, the eggs were in strand in a single column, the eggs spaced ca. 4.5 mm. apart. Twelve hours after collection, the embryos were in neural fold stage of development (Stage 14 of Limbaugh and Volpe, 1957). The embryos hatched November 10 and 11. By December 19 (i.e., 39 days after hatching began) one larva had both fore limbs erupted, though the oral apparatus was still larval. Two days later several had completely resorbed the tail and had transformed mouths; snout-vent length measured 7.0 mm.

Ecological notes.—*Bufo biporcatus* occurs in a variety of habitats in Borneo. The distribution of those for which details are available is: village clearing—four; rubber plantation—two; pepper garden—one; secondary growth—18; logged rain forest—nine; virgin primary rain forest—25. Though more active at night, these toads may be seen hopping on the forest floor by day.

This toad is much more abundant at low elevations (within 150 meters of sea level) than at high ones, at least in Borneo. Five of the Bornean toads seen were caught on Mount Kina Balu but at unknown elevations. Smith (1931A) lists *biporcatus* as occurring "above 3000 feet" (915 meters) on Kina Balu.

Males were observed calling at night around the edges of small rain-filled pools in April, May, August, and September. Females with enlarged pigmented ova were caught in May, June, and July.

Range.—Eastern Sumatra, Borneo, and the Natuna Islands.

SABAH: Beaufort District, Marabah; Kinabatangan District, Bukit Kretam, Deramakot; Kota Belud, Mount Kina Balu; Labuan District, Labuan (van Kampen, 1923); Sandakan District, Sandakan, Sapagaya Forest Reserve, Sepilok Forest Reserve; Sipitang District, Sipitang; Tawau District, Kalabakan. SARAWAK: First Division, Bidi, Mount Gadin, Kuching (*ibid.*), Matang, Sadong, Samunsan valley; Second Division, Lupar River, Saribas; Third Division, Mengiong River, Mount Dulit; Fourth Division, Baram River, Niah. KALIMANTAN: Bandjermasin, Bulungan, Buntok, upper Mahakam River, Semberra River, Sintang, Bluu.

Bufo quadriporcatus Boulenger

Bufo quadriporcatus Boulenger, 1887, Ann. Mag. Nat. Hist., (5), **19**, p. 347, pl. 10, fig. 4—Malacca; 1891, *ibid.*, (6), **8**, p. 292; 1892, Proc. Zool. Soc. London, **1892**, p. 508; 1912, Fauna Malay Penin., Rept. and Batr., p. 274; Bartlett, 1895, Sarawak Note Book, **1**, p. 13; Peracca, 1899, Rev. Suisse Zool., **7**, p. 330; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 87; Smith, 1925, Sarawak Mus. Jour., **3**, p. 30 (part).

Material examined.—Borneo 38 (1 AMNH; 1 BM; 6 FMNH; 3 MCG; 1 NHMW; 1 RMNH; 14 SM; 4 SNG; 7 ZMB); Sumatra 4 (2 NMB; 2 SNG); Malaya 2 (BM, including holotype).

Taxonomic notes.—The differences between *quadriporcatus* and *divergens* (or any other form of *biporcatus*) were understated by Boulenger (1912) and van Kampen (1923), who noted only that *divergens* had a relatively longer tibia and angular rather than straight cranial crests. About one-third of the *quadriporcatus* I examined have

slightly curved supraorbital crests and the remainder straight ones; straight crests occur in about one-third of the *biporcatus divergens* seen and curved or angulate ones in the remainder. The tibia varies from 0.33 to 0.42 of snout-vent in 20 *quadriporcatus*, but in only one does the ratio exceed 0.40. In *biporcatus divergens* the ratio is usually larger than 0.40, only five of 27 falling below that level (Table 8).

The most striking difference between these two forms is in the shape of the parotoid gland, which is invariably elongate, narrow, parallel-sided, and raised above the back a distance about equal to its width in *quadriporcatus* (fig. 16C) and triangular or oval, shorter, and not as high above the back in *b. divergens* (fig. 16D). The parotoid of *quadriporcatus* is usually longer than the eye and snout combined, whereas that of *b. divergens* is always shorter and is usually shorter than the distance from the nostril to the rear of the eye. The ratio of parotoid length to snout-vent is 0.175–0.252 (7 less than 0.20) in 20 *quadriporcatus* and 0.088–0.183 (4 above 0.16) in 29 *b. divergens*.

All *b. divergens* seen have a black interorbital bar or black spots or black chevrons on the back. No *quadriporcatus* seen, regardless of size (20.0–61.8 mm.) or locality, has black dorsal markings.

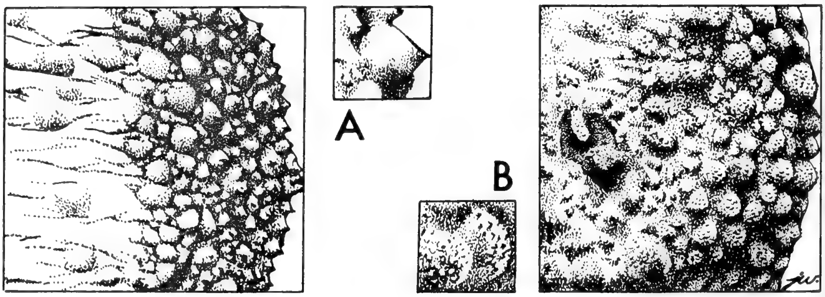


FIG. 18. Segment of skin of back and side in *Bufo quadriporcatus* (A), and *B. biporcatus divergens* (B). Insets show details of spinosity of lateral warts.

Bufo quadriporcatus is much more spinose ventrally than *biporcatus*, a difference more easily seen than described. The inner edge of the tarsus bears three to six large black spines in both species, but the bases of these spines are larger than the outer metatarsal tubercle in *quadriporcatus* and smaller than that in *biporcatus divergens*. Just below the dorsolateral edge of the body *quadriporcatus* has numerous, long black spines. As the back has very low, smooth warts, it contrasts sharply with the spinose side (fig. 18A). The lateral warts of

b. divergens also bear spines (fig. 18B), though they are not as long as those of *quadriporcatus*. Since the dorsal warts of *b. divergens* are higher than those of *quadriporcatus*, the side does not contrast with the back as sharply as in the latter.

Finally, *quadriporcatus* appears to be larger than *b. divergens*. The single adult male of the former seen measures 48.4 mm. and the two females with enlarged ova 58.8 and 61.4 mm. Seven additional females measure 52.5–63.0 mm. The largest adult male of *divergens* examined measures 42.7 and the largest female 52.0 mm. (Table 8).

Both species are known from Samunsan, Mount Dulit, and Niah, Sarawak and from Sipitang, Sabah.

Description.—A moderate-sized *Bufo*, adults to about 62 mm.; body stocky, limbs short and moderately thick; head with a pair of high, continuous supraorbital-parietal crests, usually parallel and straight; a raised supratympanic crest; head as wide as long; snout obtusely pointed, projecting and oblique in profile, longer than diameter of eye, nostril near tip of snout; canthus sharp; lores vertical, not concave; interorbital wider than upper eyelid; tympanum distinct, three-fourths of or equal to diameter of eye.

Fingers moderately long, tips blunt, not swollen; first longer than second; subarticular tubercles conspicuous, simple; supernumerary metacarpal tubercles present. Tips of toes like those of fingers; fourth toe much longer than third which is longer than fifth; third and fifth toes with 1½–2 phalanges free of web, fourth with four; subarticular tubercles simple, smaller than metatarsal tubercles; inner metatarsal tubercle oval, shorter than first toe; a smaller, circular, outer metatarsal tubercle; no tarsal ridge; a row of enlarged tarsal spines, the base of each larger than outer metatarsal tubercle; tibia 0.33–0.42 of snout-vent (median 0.372).

Top of head with numerous conical spines; back smooth or with low rounded warts; sides with elevated, spinose warts; dorsolateral warts usually tipped with one to three melanic spinules (fig. 18A); ventrally coarsely granular, each granule bearing three to seven melanic spinules; limbs spinose; parotoid elongate, very narrow, sharply raised above back, separated from eyelid; length of parotoid 0.175–0.252 of snout-vent (median 0.205; N = 20); width of parotoid 0.15–0.32 of its length (median 0.20; N = 20); an oblique row of enlarged lateral warts follows parotoid.

Color (in alcohol) dark reddish brown above and on sides; no dark, dorsal markings; lips with dark bars; ventrally yellowish brown, with or without dark spots.

Secondary sex characters.—A single adult Sumatran male (SNG 3421) has a median subgular vocal sac with one slit-like opening on the left side of the mouth. This male measures 48.4 mm. The two gravid females seen measure 58.8 and 61.4 mm.

Ecological notes.—Five specimens were caught in primary forest, two of them in small stream beds and three on the forest floor. All five were found within 150 meters of sea level.

Range.—Malaya, Sumatra, and Borneo.

SABAH: Sipitang District, Sipitang. SARAWAK: First Division, Kuching, Bukit Lintang, Pueh, Sadong, Samunsan valley, Saratok (Smith, 1925B), Tambak, Mount Temiang; Second Division, Simanggang; Third Division, Mount Dulit; Fourth Division, Baram River, Niah. KALIMANTAN: Semitau.

Bufo asper Gravenhorst

Bufo asper Gravenhorst, 1829, Delic. Mus. Zool. Vratislava, fasc. 1, p. 58—Java; Schlegel, 1837–44, Abbild. neuer Amph., p. 63, pl. 20, fig. 1; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 313 (part); 1892, Proc. Zool. Soc. London, **1892**, p. 508 (part); Mocquard, 1892, Mem. Soc. Zool. France, **5**, p. 195; Bartlett, 1895, Sarawak Note Book, no. 1, p. 13; Brown, 1902, Proc. Acad. Nat. Sci. Philadelphia, **1902**, p. 183; Andersson, 1923, Meddel. Zool. Mus. Kristiania, no. 7, p. 121; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 82 (part); Smith, 1925, Sarawak Mus. Jour., **3**, p. 30; de Witte, 1933, Bull. Mus. Roy. Hist. Nat. Belgique, **9**, no. 24, p. 7.

Nectes obscurus Barbour, 1904, Proc. Biol. Soc. Washington, **17**, p. 51—Sarawak.

Bufo obscurus Barbour, 1912, Mem. Mus. Comp. Zool., **44**, p. 75, pl. 6, fig. 20.

Material examined.—Borneo 170 (3 BM; 131 FMNH; 2 MCZ, types of *obscurus*; 26 RMNH; 8 SM); Sumatra 4 (1 FMNH; 1 NMB; 2 SNG); Java 16 (2 RMNH, types of *asper*; 14 ZMA); Malaya 8 (FMNH); Thailand 5 (NMB).

Taxonomic notes.—Gravenhorst explicitly based his description of *asper* on Javan material collected by Kuhl and van Hasselt and deposited in the Rijksmuseum, Leyden. The largest of the four (RMNH 2172) is here designated as the lectotype. Its measurements are: snout-vent 51.5 mm., head width 17.9, tibia 24.3, diameter of eye 7.0, diameter of tympanum 2.3, length of parotoid 5.2, width of parotoid 4.1.

The types of *Bufo obscurus* (Barbour) are identical in all diagnostic characters with *asper*.

Relations with *B. juxtasper* have been discussed elsewhere (Inger, 1964).

Description.—A large *Bufo*, adults to more than 120 mm.; habitus moderately stocky; limbs relatively long; head wider than long, width 0.326–0.354 of snout-vent (median 0.346; N = 13); head usually with low supraorbital crest, no parietal crest; a thick supratympanic crest separating parotoid and eyelid; snout truncate or obtusely pointed, vertical in profile or projecting slightly; nostril at end of snout; canthus rounded, distinct; lores vertical, not concave; interorbital wider than upper eyelid; tympanum distinct, about one-third diameter of eye.

Fingers moderately long; tips swollen but not wider than other parts of fingers; first finger usually slightly longer than second; subarticular tubercles large, simple; supernumerary metacarpal tubercles present. Tips of toes like those of fingers; third slightly longer than fifth; all toes except fourth webbed to swollen tips, fourth toe with 1–2 phalanges free; subarticular tubercles conspicuous, round, simple; inner metatarsal tubercle low, oval, half length of first toe; outer metatarsal tubercle round or oval, smaller than inner; a sharp tarsal ridge; tibia 0.438–0.501 (median 0.464; N = 13).

Skin of back with large round warts; skin between warts with numerous small tubercles; top of head, sides, and dorsal surfaces of limbs with many small, conical warts; most of warts and many small tubercles with melanic tips; one or two large, conical rictal warts; ventrally coarsely granular, granules usually tipped with melanin; parotoid round or subtriangular, its width 0.52–1.00 of its length (median 0.67; N = 22), its length 0.070–0.112 of snout-vent (median 0.090; N = 23; see also fig. 16H).

Color (in alcohol) dark brown above, immaculate or (in juveniles) with a few black spots; ventrally yellowish brown, usually throat, chest, and underside of legs spotted with black.

Secondary sex characters.—Females become larger than males. Six Bornean females having mature oviducts (none have mature ova) measure 95.2–120.8 mm. (mean 102.68 ± 3.77). Twelve Bornean males having nuptial pads measure 69.5–98.2 mm. (mean 83.02 ± 2.49).

Males have median subgular vocal sacs usually having paired slit-like openings (Inger, 1964). The nuptial pads consist of clusters of minute black spines covering the medial surface of the inner palmar tubercle, the dorsal and medial surfaces of the first finger from the middle of the metacarpal to the middle of the terminal phalanx, and the medial edge of the second finger.

Larvae.—Van Kampen (1910B, 1923) and Smith (1930) referred torrent-adapted tadpoles to *B. asper* but did not give reasons for their identifications. The larvae they described had ventral oral disks and greatly expanded lips, and are very similar to *Ansonia* tadpoles.

Ecological notes.—Literally hundreds of adults were collected or observed on the banks of small streams (ca. 7–20 meters wide) and rivers (width in excess of 30 meters). All of these streams flowed through rain forest; the bank vegetation of the rivers was usually logged forest, that of the small streams virgin rain forest.

Most of the animals examined came from less than 200 meters above sea level. Smith (1925B) recorded *asper* from 1525 meters on Mount Dulit, but as he did not distinguish between *asper* and *juxtasper,* the altitude cannot be confidently attributed to *asper.* Both species occur on Mount Dulit.

Geographic variation.—Javan toads have slightly longer parotoids than do those from Borneo, Sumatra, or the mainland (Table 9). The parotoid in Javan toads is equal to or slightly longer than the diameter of eye, whereas it is usually shorter than the diameter of the eye in other populations. The ratio of parotoid width to length is approximately the same in Javan (0.55–0.79, median 0.69) and Bornean toads (0.52–1.00, median 0.67).

TABLE 9.—Geographic variation in body proportions of *Bufo asper.*

Locality	No.	Range	Median
		Parotoid length[1]	
Java	15	94–183	134
Borneo	23	70–112	90
Sumatra	4	89–138	98
Thailand	2	92–130	111
Malaya	3	59–133	84
		Head width[1]	
Java	12	333–408	358
Borneo	13	326–354	346
	U[2]=29.5	P=0.01	

[1] In terms of thousandths of snout-vent.
[2] Of Mann-Whitney U test.

Javan and Bornean toads differ in head width (Table 9), but not in relative length of tibia, diameter of eye, or in diameter of tympanum.

Range.—Peninsular Thailand and Burma (Bourret, 1941) to Java and Borneo.

SABAH: Kinabatangan District, Deramakot; Ranau District, Ranau; Sandakan District, Sandakan; Tawau District, Kalabakan. SARAWAK: First Division, Samunsan valley; Second Division, Mount Klingkang; Third Division, Baleh River near mouth of Putai River, Mengiong River, Mount Dulit; Fourth Division, Baram River and Miri (Brown, A. E., 1902), Melana, Niah. KALIMANTAN: Bluu, Nanga Raun, Pulau, Puruk Tjahu (de Witte, 1933), Sanggau, Sebruang (Mocquard, 1892), Semitau, Sungei Sibau, Sungei Simiai, Sintang, Tumbang Maruwei (Andersson, 1923).

Bufo juxtasper Inger

Bufo juxtasper Inger, 1964, Fieldiana, Zool., **44**, p. 154—Kalabakan, Tawau District, Sabah.

Bufo asper Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 313 (part); 1892, Proc. Zool. Soc. London, **1892**, p. 508 (part); Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 158; Smith, 1931, Bull. Raffles Mus., no. 5, p. 30 (not of Gravenhorst).

Material examined.—Borneo 58 (2 BM; 53 FMNH; 2 RMNH; 1 SM).

Description.—A very large toad; adults to more than 200 mm., habitus stocky, limbs relatively long; head wider than long, width 0.335–0.379 of snout-vent (median 0.354; N = 13); head with thick supratympanic crest separating parotoid and eyelids; a thick supra-orbital but no parietal crest; snout obtusely pointed; nostril at end of snout; canthus rounded; lores vertical, not concave; interorbital wider than upper eyelid; tympanum distinct except for posterior rim, less than one-third diameter of eye.

Fingers moderately long; tips swollen but not wider than other parts of fingers; first finger equals second; subarticular tubercles large, simple; supernumerary metacarpal tubercles present. Tips of toes like those of fingers; third toe slightly longer than fifth, fourth much the longest; all toes except fourth webbed to swollen tips, fourth toe with 1½ phalanges free; subarticular tubercles conspicuous, round, simple; inner metatarsal tubercle low, oval, about three-fourths length of first toe; outer metatarsal tubercle round, almost as large as inner one; a sharp tarsal ridge; tibia 0.424–0.484 of snout-vent (median 0.456; N = 12).

Skin of back, sides, and legs with large, round warts; skin between large warts with few small tubercles; upper eyelids and sides of head with many small warts; warts of head, trunk, and limbs each tipped with a melanic spinule; a large, conical rictal wart; ventrally coarsely

granular, each granule with a melanic tip; parotoid oval, as long as its distance from tip of snout, its width 0.30–0.48 of its length, its length 0.175–0.256 of snout-vent.

Color (in alcohol) blackish brown above, yellowish brown below; no markings.

Secondary sex characters.—Females reach larger sizes than males. Males having vocal sacs range from 85.8–122.0 mm. snout-vent. Three males, 80.3–87.4 mm., lack vocal sacs and are probably immature. Five of the females examined fall in the size range 122–170 mm. According to Boulenger (1892), his 215 mm. specimen was a female.

Males have median subgular vocal sacs having a single, slit-like opening that may be on either side of the mouth. The nuptial pads consist of black clusters of fine spinules covering the dorsal and medial surfaces of the first finger from the middle of the metacarpal to just beyond the base of the distal phalanx, the medial face of the inner palmar tubercle, and the dorsal surface of the second finger from its base to the end of the basal phalanx.

Ecological notes.—*Bufo juxtasper* has been found in a variety of situations. Of the 15 collected in eastern Sabah in forested areas, 11 were caught in primary rain forest, one in a camp clearing, and three in secondary growth. Nine of the 15 were caught on banks of streams.

A series of 44 was collected in the agricultural regions of western Sabah. Five of these were found in wet grassy areas and 39 in flooded rice fields. The altitudinal range is moderate, extending from near sea level to about 1000 meters.

Range.—Borneo and Sumatra.

SABAH: Jesselton District, Menggatal; Kinabatangan District, Deramakot; Kota Belud District, Ranau; Tawau District, Kalabakan. SARAWAK: Second Division, Lupar River valley; Third Division, Mengiong River and Sungei Laie in Baleh River valley, Mount Dulit; Fourth Division, Bario, Long Lelang, Pa Main, Tutoh River; Fifth Division, Pa Brayong. KALIMANTAN: upper Mahakam River, upper Sibau River, Long Lanuk.

Bufo melanostictus Schneider

Bufo melanostictus Schneider, 1799, Hist. Amph., **1**, p. 216—East Indies; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 306; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 80; Smith, 1925, Sarawak Mus. Jour., **3**, p. 29.

Bufo gymnauchen Bleeker, 1858, Nat. Tijds. Ned.-Indië, **16**, p. 46—East Indies (probably Riouw Archipelago); van Kampen, *op. cit.*, p. 81.

Bufo longicristatus Werner, 1903, Zool. Anz., **26**, p. 252—Borneo.

Material examined.—Borneo 39 (9 FMNH; 7 RMNH; 12 SM; 11 UMMZ); Riouw Archipelago 2 (ZMA); Singapore 4 plus 2 larvae (FMNH); Thailand 12 (FMNH); Formosa 20 (FMNH); "East Indies" 1 (RMNH, cotype of *gymnauchen*).

Taxonomic notes.—After examining the cotype of *gymnauchen* Bleeker, I am obliged to agree with Boulenger (1882) that Bleeker's species is a synonym of *melanostictus.* Van Kampen (1923) retained the separation of the two forms, stating that the difference lay in the smoother back and tarsal ridge of *gymnauchen.*

The rugosity of dorsal skin shows sexual dimorphism in *B. melanostictus*; males have relatively smooth backs and females spinose ones with the warts more elevated (see *Secondary sex characters* below). This pattern of variation can be seen in the two specimens (ZMA 5182) from the Riouw Archipelago, the presumed type locality of *B. gymnauchen.*[1] The cotype examined (RMNH 3971) is a male and has a smooth back.

The male of the Riouw pair has no tarsal ridge, whereas the female has a low crenulated one. The cotype has a row of conical spines whose confluent bases form a low tarsal ridge. In Bornean and Singapore toads the development of the tarsal ridge varies from the condition seen in the cotype to that common in Thailand and Formosan toads, which usually have a row of distinctly separated, conical spines in place of a tarsal ridge.

Description.—A large species of *Bufo,* both sexes to more than 80 mm.; habitus stocky; head with low canthal crests, elevated supraorbital and supratympanic bony crests, no parietal crests; head wider than long, width 0.37–0.41 of snout-vent; snout obtusely pointed, vertical in profile; nostril near tip of snout; canthus sharp; lores oblique, not or weakly concave; interorbital wider than upper eyelid; tympanum distinct, about half diameter of eye.

Fingers blunt; first equal to or shorter than second; subarticular tubercules conspicuous, usually cardioid or paired; supernumerary metacarpal tubercles present. Tips of toes like those of fingers; fourth toe much longer than third or fifth; third slightly longer than fifth; toes more than half webbed; third and fifth toes usually with one phalanx free of web; fourth toe with three phalanges free; sub-

[1] The original description stated that part of the collection came from a M. Netscher from the Riouw Archipelago and part from E. F. Meijer and H. Raat (no locality given). Boulenger (1882) listed a type of *B. gymnauchen,* purchased from Bleeker and having the locality "Bintang" (=Pulau Bintan, Riouw Archipelago).

TABLE 10.—Sex dimorphism in *Bufo melanostictus* from Borneo.

		Snout-vent length[1]	
	No.	Range	Mean
Females	9	65.6–86.6	75.19±2.09
Males	10	57.2–83.8	68.52±2.78
		Head width[2]	
	No.	Range	Median
Females	8	384–410	401
Males	7	370–403	386
	U[3]=11	P=0.03	
		Tibia length[2]	
	No.	Range	Median
Females	7	329–380	363
Males	7	344–380	353
	U[3]=22	P >0.30	

[1] Of all females as large as or larger than smallest containing ripe ova; of all males having vocal sacs and nuptial pads.

[2] In terms of thousandths of snout-vent.

[3] Of Mann-Whitney U test.

articular tubercles conspicuous, simple; inner metatarsal tubercle oval, shorter than first toe; outer metatarsal tubercle smaller than inner; usually no tarsal ridge, but bases of inner row of conical spines may fuse to form a ridge; tibia 0.33–0.38 of snout-vent.

Skin of back with large round warts, sides with smaller ones, warts of both areas varying according to sex (see below); skin below coarsely granular, each granule tipped with melanic spinule in females; parotoid ellipsoidal, usually beginning above posterior rim of tympanum, separated from eyelid by supratympanic crest; length of parotoid 0.19–0.23 of snout-vent (median 0.218; N=10).

Color (in alcohol) brown above, the cranial crests and (in females) dorsal warts tipped with black; below pale brown or yellow, immaculate or with dark spots.

Secondary sex characters.—Pope (1931) found females to be larger than males in Fukien Province, China. His 10 largest males measured 65–72 mm. (mean 67.8) and the 10 largest females 74–85 mm. (mean 78.3). Although the Bornean females are slightly larger than males (means 75.19 and 68.52 mm., respectively), the difference in this small sample is not statistically significant (Table 10). Bornean females have relatively wider heads than males; the sexes do not differ in length of tibia (Table 10).

Females, besides having the dorsal and lateral warts more elevated than those of males, have distinct melanic spines, especially

on the lateral warts. In all males having nuptial pads, the dorsal and lateral warts are low and devoid of spines. Mature males usually lack the ventral spinules found in females. An immature male (FMNH 61009) lacking both nuptial pads and vocal sacs has dorsal and lateral spines as in mature females. Apparently the same pattern of hormonal control of dorsal and lateral spinosity occurs in *melanostictus* as in African *B. funereus* (Inger and Greenberg, 1956).

Pope (1931) did not "detect any difference between the sexes in . . . texture of the skin" in *melanostictus* from southeastern China. Although female toads from China are not as spinose as those from Thailand, Malaya, or Borneo, the Fukien Province toads I have examined (FMNH 24428–37) do show sex dimorphism in spinosity. Males having fully developed nuptial pads have no lateral spines. The difference between the sexes in the Chinese sample is especially conspicuous in the area below the parotoid gland.

Males have median subgular vocal sacs with single slit-like openings that may be on the right or left side of the mouth. The vocal sac and its investing muscles are black, the gular skin is not. The nuptial pad at its maximum development consists of black spinules covering dorsal and medial surfaces of the first finger from the wrist to the tip of the finger, dorsal and medial surfaces of the second finger for its entire length, and medial edge of the third finger. Lineae masculinae are absent.

Larvae.—Singapore larvae seen agree with published descriptions (Boulenger, 1912; van Kampen, 1923).

Body ellipsoidal; mouth ventral, subterminal; oral disk with papillae at sides only; beaks smooth, black near edges only; labial teeth I:1–1/III; spiracle sinistral, below line between eye and root of hind limb; anus median; tail leaf-like, margins subparallel, tip broadly rounded, fins deeper than caudal muscle beyond basal third of tail; total length at Stage X 18.2 mm. (1 specimen), at Stage XVIII 20.3 mm. (1).

Color black above, lighter below; caudal muscle black, fins dusky; no conspicuous markings.

Ecological notes.—In Borneo *melanostictus* is confined to large villages and towns. Presumably it occurs also in cultivated areas surrounding towns, though I have no records of such occurrence.

In Java Church (1959) found *melanostictus* in towns in open places, in gardens, and in roadside ditches. Church rarely found this toad in flooded rice fields, in swampy ground, or in fields of tall grass.

All Bornean localities are at or near sea level. In Java *melanostictus* is more widely distributed near sea level but does occur at elevations as high as 800 meters (*ibid.*). Van Kampen (1923) stated that it occurs from sea level to ". . . high up in the mountains," but the highest elevation given by van Kampen is 300 meters.

Bufo melanostictus breeds the year round in Bangkok (Smith, 1917) and in Java (van Kampen, 1923; Church, 1960A). Given the favorable climate of coastal Borneo, *melanostictus* should be able to breed year round there.

Range.—India and southern China to Bali (Church, 1959) and Borneo.

SARAWAK: First Division, Kuching, Lundu, Matang (Smith, 1925B), Santubong, Satang Island; Third Division, Kapit; Fourth Division, Baram (van Kampen, 1923). KALIMANTAN: Bandjermasin (*ibid.*), Balikpapan, Pontianak, Singkawang.

Cacophryne Davis

This genus has recently been shown to be a Bufoninae (in the restricted sense), having a Bidder's organ and a supraotic squamosal arm (Griffiths, 1959). Brongersma (1935) and Griffiths have shown that, contrary to Davis's statement (1935), the pectoral girdle of *Cacophryne* is arcifero-firmisternal.

Davis (*ibid.*, p. 87) said that the testis of *borbonica* is not elongate as in other toads. In two males of *borbonica* the ratios of testis length to snout-vent length were 5.4:27.4 mm. (FMNH 121758) and 5.5:27.5 mm. (FMNH 121754). In a male of *C. cruentata* (RMNH 6482) the ratio was 7.0:27.5 mm. In an adult male (nuptial pads present) of *Bufo biporcatus divergens* (FMNH 77455) the ratio was found to be 5.0:40.0.

In most of the characters tabulated by Tihen (1960), *Cacophryne* resembles *Ansonia* and *Pseudobufo*, which, according to Tihen, lie somewhere between the more generalized *Bufo* and the more specialized *Pelophryne*. *Cacophryne* has eight presacral vertebrae and a freely movable coccyx as in *Bufo* (and in *Ansonia* and *Pseudobufo*), but an elongate tensor fasciae latae and an incomplete quadratojugal as in *Pelophryne* (and most *Ansonia* and *Pseudobufo*). The ova are rather large as in *Ansonia* (small in *Pseudobufo*), but are pigmented as in *Pseudobufo* (non-pigmented in *Ansonia*).

The larva of *Cacophryne cruentata*, if associated with the correct adults by Schijfsma (1932) and Brongersma (1935), has a small oral

disk characteristic of non-specialized bufonid larvae (and, hence, different from that of *Ansonia*), but has the lower lip completely bordered by papillae, which thus differentiate it from the known larvae of *Bufo*, *Pedostibes*, and *Pelophryne*.

The principal morphological distinction between adult *Cacophryne* and other Indo-Malayan bufonids lies in the pectoral girdle (arcifero-firmisternal in *Cacophryne* only).

Cacophryne cruentata has more extensive webbing than *borbonica*; in *cruentata* the web extends beyond the distal subarticular tubercles of the third and fifth toes, whereas in *borbonica* it rarely reaches those tubercles. The vent is close to the end of the coccyx (i.e., opens at the dorso-posterior aspect of thighs) in *borbonica*, but opens at the end of a long tube (i.e., near ventro-posterior aspect of thighs) in *cruentata*.

Cacophryne borbonica (Tschudi)

Hylaplesia borbonica Tschudi, 1839, Mem. Soc. Sci. Nat. Neuchâtel, **2**, p. 70—"East Indies," here restricted to Java.[1]

Cacophryne borbonica Davis, 1935, Field Mus. Nat. Hist., (Zool.), **20**, p. 88, fig. 8.

Bufo borbonicus Cope, 1867, Jour. Acad. Nat. Sci. Philadelphia, **6**, p. 193; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 286 (part).

Nectophryne borbonica van Kampen, 1923, Amph. Indo-Austr. Arch., p. 70, fig. 7.

Bufo borbonica Smith, 1925, Sarawak Mus. Jour., **3**, p. 30.

Bufo jerboa Boulenger, 1890, Proc. Zool. Soc. London, **1890**, p. 328, pl. 25, fig. 3—southeastern Borneo.

Nectophryne sumatrana van Kampen, 1910, Natuurk. Tijds. Ned.-Indië, **69**, p. 19, pl. 1, fig. 1—Bandar Bahru, Sumatra.

Material examined.—Borneo 17 (1 BM, holotype of *B. jerboa*; 4 FMNH; 1 MCG; 1 NMB; 10 SM); Java 3 (RMNH, 2 cotypes of *borbonica*); Sumatra 18 (1 FMNH; 2 MCZ; 2 NHMW; 10 RMNH; 3 ZMA, including type of *N. sumatrana*); Thailand 6 (1 FMNH; 3 MCZ; 2 ZMA).

Taxonomic notes.—Examination of the types of *borbonica* and *Bufo jerboa* Boulenger leads me to support Smith's opinion (1930) that they are conspecific. The peculiarly enlarged subarticular tubercles of the feet, the color pattern, the extent of webbing, and the presence

[1] As Tschudi based his description on Boie's manuscript, the latter's specimens, which are the types, establish the type locality. The Leiden Museum has two specimens (RMNH 1739) collected by H. Boie and Macklot in Java.

of large glands in the skin of palm and sole[1] of the holotype of *jerboa* indicate its close relationship to *borbonica*.

The glands just mentioned are better developed in males from Sumatra and Borneo than in those from Java and Thailand (see pp. 77 and 78 for details).

TABLE 11.—Size variation in *Cacophryne borbonica*.

Males[1]				Females[2]				
Thailand	Sumatra	Locality[3]	Borneo	Thailand	Java	Sumatra	Locality[3]	Borneo
26.1	22.1	P–T	27	32.0 o	28.0 +	27.2 +	P–T	30.0 j
26.6	22.7	P–T	29		34.7 o	27.8 +	P–T	30.6 j
27.3	26.0	Ps	30			28.9 j	?	
27.4	26.1	Ps	31			37.0 +	B	40 o
28.5	26.5	Ps				37.4 o	Ps	40 +
	27.0	Ps				39.4 o	Ps	41 +
	27.1	Ps				39.5 o	?	44 +
	27.5	Ps						45 +
	28.1	Ps						45 +
	29.2	Ps						47 o

[1] All have vocal sacs and nuptial pads.

[2] Those followed by + have enlarged ova, those by o have not, and those by j have immature oviducts.

[3] P–T = Padang–Talakmau area; Ps = Pasemah in southern Sumatra; B = Bandar Bahru in northern Sumatra; ? = no definite locality.

Snout-vent length varies more than usual for small toads (Table 11). On Sumatra size range is not only extensive, but also appears to be bimodal, the Padang-Talakmau toads being distinctly smaller than those from Bandar Bahru and Pasemah 275 and 600 kilometers to the north and south, respectively, of the Padang area. The presence of eggs in females and nuptial pads in males show that the difference in size is probably not dependent on age. The "small" females from Sumatra lack supernumerary metacarpal tubercles which are present in the larger females. Otherwise, the small and large Sumatran toads are similar and are probably conspecific.

The dorsal pattern varies from a few widely separated black spots (van Kampen, 1910A, pl. 1, fig. 1) to a large black, complex marking (van Kampen, 1923, fig. 7). This variation is not correlated with any other character, and both patterns may occur at one locality. Despite the bimodality in size in Sumatra and the differences in development of the plantar mucous glands, all of these populations seem to be conspecific.

[1] Miss A. C. G. Grandison of the British Museum kindly checked this character in the holotype of *jerboa*.

Description.—A small to moderate-sized bufonid, males to 30 mm., females to near 50 mm.; habitus slender; limbs long, slender; head without bony crests, about as wide as long, head width 0.23–0.30 of snout-vent; snout truncate or pointed, projecting, oblique in profile, equal to or shorter than eye; nostril much nearer to tip of snout than to eye; canthus rostralis sharp; lores vertical, straight; interorbital width greater than width of upper eyelid; tympanum distinct, about one-third diameter of eye.

Fingers long; tips swollen into small round disks; first slightly shorter than second; no webbing on hand; subarticular tubercles conspicuous, large; supernumerary tubercles on metacarpals usually present in females, present or absent (or inconspicuous) in males. Tips of toes same shape and size as those of fingers; toes about half webbed; first two toes with one, third and fifth toes with 2–2⅔, and fourth toe with 3½–4 phalanges free of broad webbing; inner metatarsal tubercle oval, outer one smaller and round; subarticular tubercles conspicuous, basal ones on at least third and fourth toes as large as inner metatarsal tubercle (fig. 15A); tibia 0.56–0.70 of snout-vent.

Skin above with numerous, small, heterogeneous warts; parotoid consisting of a pair of short oval glands in line or a more or less continuous, long, dorsolateral gland; throat finely granular in males, coarsely granular in females; rest of ventral surface coarsely granular in both sexes; a row of two to five (usually four or five) enlarged, conical tubercles on outer surfaces of lower arm and tarsus.

Color (in alcohol) pale or dark brown above and on sides; dorsolateral light stripe usually present in darker specimens; pairs of dark spots in interorbital and occipital regions; back with a small dark sacral cross, with two pairs of small dark spots, or with a large, double cruciform marking; limbs with dark crossbars; ventrum yellowish, usually with dark brown suffusion anteriorly.

Secondary sex characters.—Though snout-vent length varies geographically, females from any given area are larger than sympatric males (Table 11).

Males have median subgular vocal sacs having one or two long, slitlike openings. A brownish nuptial pad covers the dorsal surfaces of the basal phalanx and the distal half of the metacarpal of the first finger.

Males have clusters of mucous glands in the skin of the palms and soles. Histological sections of the skin from the palm were pre-

pared from three males, two from Sumatra (RMNH 5068–9) and one from Thailand (FMNH 121758). In the last, the glands are grouped in twos and threes and a typical large gland measured 75×130 micrometer units as compared to 15 units for the thickest overlying epidermis. In the Sumatran males the glands were clustered in groups of 8 to 14 in the transverse direction; typical large glands measured 105×135 to 150×180 micrometer units as compared to 10–15 units for the epidermis. The glands were packed with secretion and the nuclei lay at the perimeter of the glandular cells in all three specimens.

Ecological notes.—*Cacophryne borbonica* is at least more abundant at moderate elevations, if not restricted to them. Smith (1925B) recorded 15 specimens from 600–1375 meters and 11 from 900–1500 meters in Sarawak; additional Bornean toads have been caught at 900 and 1524 meters. Of the Sumatran toads for which data are available, one was caught at 1000, two at 1200, and nine at 1400 meters. The Thai specimens studied were collected in the hills southwest of Patelung.

The Bornean localities for this species, with the possible exception of the type locality of *jerboa* ("southeast Borneo"), all lie in areas of undisturbed rain forest.

Geographic variation.—The most striking variation involves the mucous glands of males. These glands are much more conspicuous and form larger clusters in males from Sumatra and Borneo than in those from Java and Thailand. The smaller glands and smaller clusters noted above in the Thailand male characterize all five seen from there. These differences are not attributable to size or age as the size range of Sumatran males completely overlaps that of the Thai males and as all males studied had vocal sacs and nuptial pads.

Geographic variation in snout-vent length in Sumatra has already been mentioned (p. 76). Apparently female toads from Borneo are larger than those from other parts of the range (Table 11).

Range.—Peninsular Thailand, Malaya, Sumatra, Java, and Borneo.

SABAH: Kota Belud District, Mount Kina Balu. SARAWAK: First Division, Mounts Penrissen and Poi; Fourth Division, headwaters of Sungei Tutoh. KALIMANTAN: "southeastern Borneo."

Pelophryne Barbour

This genus is the most distinctive and hence easily recognized of the Oriental bufonids. Its distinguishing characteristics are: rela-

tively small size (no known specimens exceed 40 mm.), coccyx fused to sacrum and expanded dorsally, at most seven presacral vertebrae, fleshy webbing on hand and foot (usually enclosing half or more of first finger), relatively enormous ova (diameter roughly ten per cent of female snout-vent length), and small (ca. 5–10) clutch size (Barbour, 1938; Tihen, 1960; Inger, 1960A). Rapid identification can be made on the basis of the webbing and the dorsal expansion of the coccyx.

Specific definition, however, is difficult and remains at the typological level. Several species, or nominal forms, are represented by local series of five or more individuals; such series exist for *albotaeniata* (Mount Balabag, Palawan), *brevipes* (Mount McKinley, Mindanao), *lighti* (Mount Malindang, Mindanao), *misera* (Mount Kina Balu, Sabah), and "*signata*" (Aor Island). In general, these series show narrow local variation in size (Table 12), webbing, form of tips of fingers, and tympanum diameter.

Coloration shows moderate local variation though the gross pattern is stable within series. For example, the Aor Island sample (BM 1940.1.28.1–4; SNM, 5 unnumbered) is characterized by a lateral yellow stripe of varying width and continuity, from below the eye to behind the arm. Ventral coloration in the same series consists of large yellow and brown spots that vary in size and in relative proportion. In the Kina Balu series of *misera*, the dorsal surface is occupied by a light area slightly constricted behind the head; some individuals have a narrow, vertebral dark streak posteriorly. Ventrally, the *misera* series is either dark brown with small yellowish spots or yellowish with brown spots.

On the basis of these series, one may recognize four or five forms differing in size, coloration, width of the digital disks, and tympanic diameter. But the relations of these forms to one another, their taxonomic level, and their relations to single specimens from other localities are difficult to determine because no two forms are known from a given locality.

The types of six of the eight species recognized by Barbour (1938) have been examined. One species, *maculatus* (Mocquard), belongs in the genus *Pedostibes* (see p. 92). Association of specimens with the two nominal forms (*brevipes* Peters and *lighti* Taylor), whose types I have not seen, has been made elsewhere (Inger, 1954A, 1960A).

The holotype of *guentheri* (Boulenger), a gravid female measuring 29.5 mm., is larger than any specimens listed in Table 12. It is approached in size by the holotype (and only known specimen) of

TABLE 12.—Local variation in snout-vent length (mm.) in adults of various forms of *Pelophryne* Barbour.

Form	Locality	Males[1]			Females[2]		
		No.	Range	Mean	No.	Range	Mean
albotaeniata	Mt. Balabag, Palawan	4	18.2–19.9	18.7	3	19.2–22.8	21.0
brevipes	Mt. McKinley, Mindanao	4	16.9–17.7	17.4	1	17.4	—
lighti	Mt. Malindang, Mindanao		—		6	17.9–18.5	18.2
misera	Mt. Kina Balu, Sabah	6	16.3–21.1	18.3	11	17.7–20.6	18.9
"*signata*"	Aor Island	4	20.2–21.7	20.7	5	22.6–25.2	24.0

[1] All having vocal sac openings.
[2] All equal to or larger than the smallest containing enlarged ova within a given series.

macrotis (28.2 mm.), but differs from the latter in having the tympanum about three-fifths the diameter of the eye instead of almost equal to the eye and in having more extensive webbing. Two adult males (AMNH 6733, MCZ 3205) measuring 30.5 and 30.2 mm. and one immature male (MCZ 3210) lacking a vocal sac and measuring 24.2 mm. are assigned to *guentheri*.

Apart from *guentheri*, the holotype of *macrotis* (Boulenger) differs from all other *Pelophryne* in being larger and in having a larger tympanum, and from *misera* and *albotaeniata* in having the outer fingers distinctly dilated at the tips. The validity of *macrotis*, based on a single individual, is doubtful.

The three types of *misera* Mocquard (MHNP 89.331–3) measure 17.1–20.8 mm., the largest being a gravid female. In size, tympanic diameter, webbing, and form of disks, these resemble the large Kina Balu series seen so closely that their association is probably reliable.

Pelophryne misera and *P. albotaeniata* Barbour of Palawan are more similar to one another than either is to any other *Pelophryne*. They are approximately the same size (Table 12), the snout has a vertical profile in both, the tips of their fingers are not wider than the basal phalanges, and males of both have numerous small, spinose tubercles dorsally. They differ somewhat in coloration (see below, p. 89).

The two types of *signata* Boulenger measure 15.1 and 15.6 mm. These females from southwestern Borneo have broadly dilated finger tips, wide interorbital (about twice the width of the upper eyelid), tympanum more than half diameter of eye, and a cruciform dorsal pattern. Except for the dorsal pattern, they are identical to three specimens from "Sarawak" (FMNH 81935; MCZ 3207, 3209), one from Mount Dulit, Sarawak (BM 1933.6.20.16), one from Selangor, Malaya (BM 1905.1.28.9), and two from Sumatra (MCG 29573; MCZ 3820). Males having vocal sacs measure 13.3–16.4 mm.; females with enlarged ova measure 15.8–17.6 mm.

Four Singapore specimens (BM 95.1.8.14, 96.6.25.97–8), including one juvenile (9.1 mm.), one adult male having vocal sacs (16.2 mm.), and two females containing enlarged ova (18.2 and 18.8 mm.), vary in dorsal coloration. One has a broad mid-dorsal yellowish brown area slightly constricted behind the head, another has a thin dark, X-shaped marking, and a third has small dark spots on a light brown ground color. They thus form a graded series between the cruciform pattern of the types of *signata* and the uniform dorsal pattern of a

"Sarawak" specimen (FMNH 81935) along one line of variation, and between the cruciform pattern of the types and the spotted dorsal pattern of the Mount Dulit specimen (BM 1933.6.20.16). In other characters the Singapore specimens agree with the types of *signata.*

Nectophryne exigua Boettger (type locality Baram River, Sarawak) is known from a single adult male (SNG 3737). Its small size (14.3 mm.), the shape of the digits, and the webbing agree with *signata.* It differs from the latter in coloration, which consists of small dark spots on a yellowish-brown dorsum and a few dark spots on a yellow venter. Exactly the same pattern occurs in the adult male from Mount Dulit mentioned above.

Roux (1906) placed *exigua* in the synonymy of *guentheri,* arguing that the holotype of *exigua* was a juvenile, that it resembled closely juveniles of *guentheri* from Singapore, and that the sole distinction (its smaller tympanum) between it and *guentheri* was a function of age. The holotype of *exigua* and the Singapore specimens Roux referred to (those mentioned in the second paragraph above) are adults with one exception. They are not only smaller than *guentheri,* but also have less webbing. Differences in tympanic diameter appear in this sample but they are sexual, the males having a smaller tympanum than the females.

In general size, shape, and size of disks, the presence of a ventrolateral yellow stripe anteriorly, and extent of webbing, *signata* resembles *brevipes* (Peters) very closely. In fact, I can find no characters to separate the Mindanao series of *brevipes* from the heterogeneous sample of *signata.* Additional material or further study may reveal means of distinguishing between these nominate forms. However, they are clearly more closely related to each other than either is to other forms of *Pelophryne.* In the absence of distinguishing characters, I propose to synonymize *brevipes* and *signata.* *Nectophryne exigua,* therefore, also becomes a synonym of *P. brevipes* (Peters).

The Aor Island series called "*signata*" in Table 12 is intermediate in size between *brevipes,* on the one hand, and *guentheri* and *macrotis,* on the other. The finger tips of the Aor specimens are shaped like those of these three forms. The size of the tympanum is about that of *guentheri* and *brevipes,* but the webbing is like that of *brevipes* and less extensive than that of *guentheri.*

Differences between *albotaeniata* Barbour and *brevipes* have been discussed previously (Inger, 1954A). *Pelophryne lighti* (Taylor) was re-evaluated and compared to *brevipes* in a later paper (Inger, 1960A).

In summary, the genus *Pelophryne* appears to consist of five valid taxa and one doubtful one: *guentheri*, a relatively large form known only from Borneo; *albotaeniata*, a small form from Palawan; *lighti*, a small form from western Mindanao; *misera*, a small form known only from northern Borneo; and *brevipes*, a widespread, variable form known from the Malay Peninsula, Sumatra, Borneo, several lesser islands in the South China Sea, and eastern Mindanao. These forms probably represent at least four valid species: *guentheri* is almost certainly a distinct species; *misera* and *albotaeniata* are certainly distinct from the others but may belong to one species; *brevipes* is specifically distinct from *misera*, *albotaeniata*, *guentheri*, and *lighti*; the last is also probably a valid species. *Pelophryne macrotis* (Boulenger) remains a doubtful taxon.

The following tentative key to the six typological species will at least provide a guide to my interpretation of these forms (fig. 19).

1A. Tips of fingers wider than basal phalanges (fig. 19A) .... 3.
 B. Tips of fingers not wider than basal phalanges (fig. 19B) .... 2.
2A. Throat immaculate, cream-colored or yellow .... *albotaeniata*.

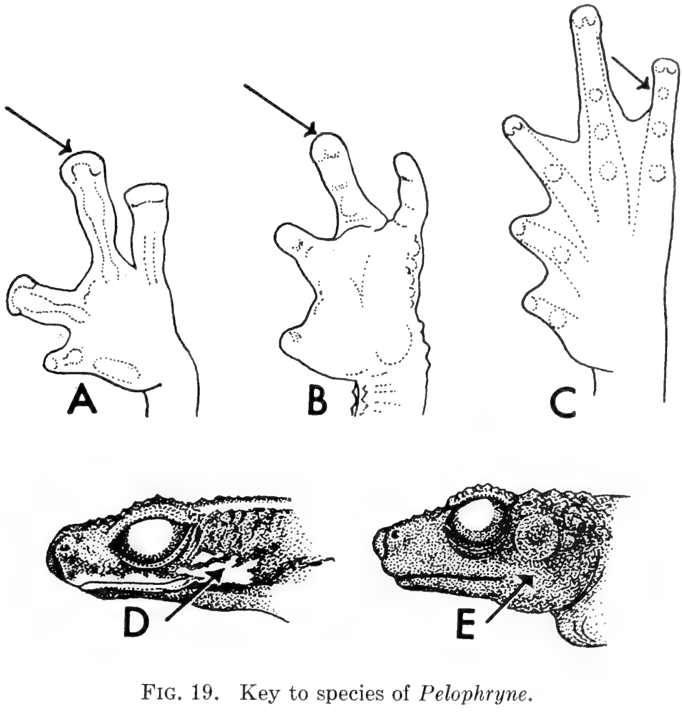


FIG. 19. Key to species of *Pelophryne*.

B. Throat spotted, yellowish spotted with brown or brown spotted with yellow or white . . . . *misera.*

3A. Tympanum at least four-fifths of diameter of eye . . . . *macrotis.*
B. Tympanum at most three-fifths of diameter of eye . . . . 4.

4A. Fifth toe webbed to disk; size large (adult females over 25 mm.) . . . . *guentheri*
B. Fifth toe with one to two phalanges free of web (fig. 19C) . . . . 5.

5A. A yellow or white stripe or row of spots on upper lip from below eye to below tympanum (fig. 19D) . . . . *brevipes.*
B. Upper lip dark, without light stripes or row of light spots (fig. 19E) . . . . *lighti.*

Pelophryne guentheri (Boulenger)

Nectophryne guentheri Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 280, pl. 18, fig. 3—Matang, Sarawak; Roux, 1906, Proc. Zool. Soc. London, **1906**, p. 62 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 68 (part).

Pelophryne guentheri Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 193 (part).

Material examined.—Borneo 4 (1 AMNH; 1 BM; holotype; 2 MCZ).

Taxonomic notes.—Some of the specimens Roux (1906) identified as *guentheri* are probably *brevipes* (see p. 82), as are three (MCZ 3207–9) of the five *guentheri* listed by Barbour (1938) and all of the *guentheri* listed by Smith (1925A, p. 13). All of these misidentified toads are adults; six females measure 15.8–22.2 mm., compared to 29.5 for the female holotype of *guentheri,* and have the webbing characteristic of *brevipes.*

Boulenger (1882) referred to the holotype as half grown. As its ova exceed 1.5 mm., it is probably mature.

Description.—A large species of *Pelophryne,* adults ca. 30 mm.; habitus slender; limbs slender; head slightly depressed; snout truncate, projecting, oblique in profile, as long as diameter of eye; nostril closer to tip of snout than to eye; canthus rostralis sharp; lores vertical; interorbital $1\frac{1}{2}$ times width of upper eyelid; tympanum conspicuous, one-half to three-fifths diameter of eye.

Tips of fingers dilated into truncate disks, those of third and fourth fingers wider than tympanum; fleshy web of hand reaching tip of first finger; two phalanges of second and fourth fingers free. Tips of toe shaped like those of fingers but not as wide; web thick, reaching tips of first three toes; fifth toe with one-half phalanx free, fourth with two free; subarticular and metatarsal tubercles weak but distinct.

Skin above with heterogeneous tubercles; some larger tubercles spinose and surrounded by ring of small whitish asperities (observed only in holotype); ventral surfaces coarsely granular.

Color (in alcohol) brown above and on sides, with small black spots usually on larger tubercles; underside yellowish with brown mottling especially heavy on throat.

Secondary sex characters.—The one adult male (MCZ 3205—30.2 mm.) assigned to this species has a median subgular vocal sac having a pair of slit-like openings, a yellowish nuptial pad on the first finger, and one row of yellow mandibular spines.

Ecological notes.—Matang, the type locality, is a hill not exceeding 1000 meters at its peak.

Range.—Known only from Sarawak, though undoubtedly occurs in adjacent parts of Borneo.

SARAWAK: First Division, Matang.

Pelophryne brevipes (Peters).

Hylaplesia brevipes Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**, p. 34—Zamboanga, Mindanao.

Pelophryne brevipes Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 194; Inger, 1954, Fieldiana, Zool., **33**, p. 236, fig. 40 (part); 1960, *loc. cit.*, **39**, p. 415, fig. 72.

Bufo brevipes Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 287.

Nectophryne signata Boulenger, 1894, Proc. Zool. Soc. London, **1894**, p. 645, pl. 40, fig. 1—Mount Rabong, Kalimantan; Roux, 1906, *loc. cit.*, **1906**, p. 63; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 70; Smith, 1925, Sarawak Mus. Jour., **3**, p. 31 (part).

Pelophryne signata Barbour, 1938, *op. cit.*, p. 193.

Nectophryne exigua Boettger, 1901, Abh. Senck. Naturf. Ges., **25**, p. 394—Baram River, Sarawak.

Nectophryne guentheri (part, not of Boulenger) Roux, *op. cit.*, p. 62; van Kampen, *op. cit.*, p. 68; Smith, 1925, *op. cit.*, **3**, p. 13.

Material examined.—Borneo 34 (4 BM, including types of *signata*; 11 FMNH; 2 MCZ; 5 RMNH; 11 SM; 1 SNG, holotype of *exigua*); Sumatra 5 (2 BM; 1 MCG; 2 MCZ); Natuna Islands 2 (BM); Mentawei Islands 2 (1 BM; 1 FMNH); Aor Island 9 (4 BM; 5 SNM); Singapore 4 (BM); Malaya 1 (BM); Mindanao 8+5 larvae (FMNH).

Taxonomic notes.—Reasons have been given above (p. 82) for placing *signata* and *exigua* in the synonymy of *brevipes*.

As noted above (p. 84), the specimens listed by Smith (1925A, p. 13) as *N. guentheri* have the size and webbing of *brevipes*.

Description.—A small species, adult males 13–23 mm., females 15–25 mm.; habitus slender; limbs slender; head depressed, as wide as body, width 0.29–0.32 of snout-vent; snout truncate, projecting, oblique in profile, subequal to diameter of eye; nostril near tip of snout; canthus rostralis distinct, usually rounded; lores vertical, not concave; interorbital 1½ to 2 times width of upper eyelid; tympanum conspicuous, about half diameter of eye.

Tips of fingers dilated into truncate disks, those of third finger equal to width of tympanum; fleshy web of hand leaving only part of the tip of first finger free, two phalanges of second and fourth fingers free; subarticular and palmar tubercles obscure. Tips of toes shaped like those of fingers but not as wide; web thick, reaching disks of first three toes, one to two phalanges of fifth toe free, fourth toe with two to three free; subarticular and metatarsal tubercles obscure; tibia 0.42–0.48 of snout-vent.

Skin above with scattered heterogeneous small tubercles; laterally and ventrally coarsely granular.

Color (in alcohol) brown above, usually darker on sides; dorsum immaculate, with small black spots, or with light or dark cruciform pattern; ventrally spotted with yellow (or white) and brown; yellow (or white) ventral color extends forward on side above axilla to below eye forming a narrow or wide, continuous or interrupted light stripe.

Secondary sex characters.—As indicated in the first line of the *Description*, the size ranges of males and females are extensive and overlap widely. In the Aor Island sample, the only one available comprising numbers of both sexes, females are distinctly, though not greatly, larger than males (Table 12).

Males have median subgular vocal sacs having slit-like openings on either or both sides of the mouth. A weak nuptial pad is present on the first finger of all males larger than 20 mm. A single row of brown or yellow mandibular spines is present in nine males (13.8–24.3 mm.) having vocal sacs, but absent in three others (13.3–15.5 mm.).

Larvae and development.—A larval series from Mindanao (FMNH 50953) has been described (Inger, 1960A). Briefly, the larvae are small (head and body 4–5 mm.), have a subterminal circular oral disk, a few labial teeth in one row on the upper lip, no teeth on the lower lip, weak beaks, no visible spiracle, a feebly coiled gut, and a leaf-like tail.

Presumably, the larva subsists on the large amount of yolk which accounts for the large ova (1.7 mm. in a 15.8 mm. female—FMNH 81935). Development is probably rapid.

Ecological notes.—In Borneo specimens of *brevipes* have been collected between 50 and 2130 meters above sea level. The species is also known from less than 200 meters above sea level at Serason, Natuna Islands and between 300 and 1400 meters on Mindanao (Inger, 1954A).

Nine specimens were found in primary rain forest, two on vegetation 0.6–1.5 m. above ground.

The ova from which the larval series (FMNH 50953) was reared, were found in a rain-filled broken bottle in primary rain forest (Inger, 1960A).

Geographic variation.—Series are available only from one locality on Mindanao and one on Aor Island. Specimens from Aor are larger than those from Mindanao (Table 12) and have less extensive webbing. One phalanx of the third toe and two of the fifth are free of web in the Aor series, whereas the web reaches the disk of the third toe (i.e., one-half phalanx free) and leaves only one phalanx free on the fifth toe in the Mindanao toads. The webbing of the hand is correspondingly reduced in Aor toads, leaving the entire disk of the first finger free; only part of the disk projects from the web in Mindanao toads.

Variation in the remainder of the sample is difficult to evaluate because each locality is represented by only one or two specimens. In general, in webbing and size these scattered specimens agree with the Mindanao series.

Dorsal coloration varies greatly (see pp. 81 and 86), but the variation may be individual as much as geographic. Only one variant—many small dark spots on a light brown back—may represent local differentiation. This pattern appears on just two specimens, the holotype of *exigua* Boettger and BM 1933.6.20.16, and both of them come from northern Sarawak ("Baram River" and Mount Dulit).

Range.—Malay Peninsula, Singapore, Aor Island, Natuna Islands, Mentawei Islands, Sumatra, Borneo, and Mindanao.

SARAWAK: First Division, Mount Penrissen (Smith, 1925B), Santubong; Third Division, Mount Dulit, Mengiong River; Fourth Division, Baram River (Boettger, 1901), Labang, Sungei Pesu, Tamabo Mountains; Fifth Division, Mount Murud. KALIMANTAN: Mount Damus, Mount Kenepai.

Pelophryne macrotis (Boulenger)

Nectophryne macrotis Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **16**, p. 171—Akar River, Sarawak; Roux, 1906, Proc. Zool. Soc. London, **1906**, p. 63, pl. 2, fig. 3; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 69.

Pelophryne macrotis Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 191.

Material examined.—Borneo 1 (BM, holotype).

Taxonomic notes.—The only differences between the holotype of *macrotis* and *guentheri* are the slightly larger tympanum of *macrotis* (almost equal to eye instead of about three-fifths diameter of eye) and the more extensive webbing of *guentheri* (to disk of fifth toe instead of leaving 1½ phalanges free). Validity of *macrotis* requires additional specimens for confirmation.

Description.—A large *Pelophryne*, adult female 28 mm.; habitus slender; limbs long and slender; head depressed; snout truncate, projecting, oblique in profile, longer than diameter of eye; nostril near tip of snout; canthus rostralis sharp; lores vertical; interorbital 1½ times width of upper eyelid; tympanum conspicuous, about four-fifths diameter of eye.

Tips of fingers dilated into truncate disks, that of third finger narrower than tympanum; fleshy web of hand leaving one-half phalanx free on first finger and two phalanges free on second and fourth fingers. Tips of toes shaped like those of fingers though not as wide; web thick; first three toes webbed to disks; fifth toe with 1½ phalanges free, fourth toe with 2½ free; subarticular and metatarsal tubercles obscure.

Skin above with heterogeneous small tubercles; coarsely granular below.

Color (according to Boulenger, 1895) olive above with black and red spots; ventrally with equal amounts of yellow and black mottling.

Range.—Known only from the Akar River, Fourth Division, Sarawak.

Pelophryne misera (Mocquard)

Nectophryne misera Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 161, pl. 11, fig. 7—"North Borneo"; Roux, 1906, Proc. Zool. Soc. London, **1906**, p. 59; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 66; Smith, 1925, Sarawak Mus. Jour., **3**, p. 14; 1931, Bull. Raffles Mus., no. 5, p. 14.

Pelophryne misera Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 193.

Material examined.—Borneo 33 (14 BM; 1 FMNH; 2 MCZ; 3 MHNP, types of *misera*; 4 NMB; 9 SNM).

Taxonomic notes.—The similarity of *misera* to *albotaeniata* has been referred to above (p. 81).

In both forms the back is occupied by a broad light area. All seven individuals of *albotaeniata* seen (FMNH 51366–72) have a narrow dark marking extending the length of the vertebral region; none of the *misera* seen have a complete dark vertebral band although a few have several dark spots mid-dorsally. As noted in the key, the coloration of the throat also differs.

If the genus were better known, *albotaeniata* would probably be made a subspecies of *misera*. Such a step now would go beyond our knowledge of the specific relations of the group.

Description.—A small species, adult males 16–21 mm., females 17–21 mm.; habitus moderately stout; limbs slender; head as wide as body, 0.31–0.36 of snout-vent length; snout truncate, vertical in profile, not as long as eye diameter; nostril closer to tip of snout than to eye; canthus rostralis sharp, concave; lores vertical, not concave; interorbital 1½ to 2 times width of upper eyelid; tympanum conspicuous, about half diameter of eye.

Tips of fingers blunt, not wider than basal phalanges; fingers with thick webbing; first finger scarcely projecting from web; second and fourth fingers with one phalanx free, third with two free of web; subarticular and palmar tubercles obscure. Tips of toes not expanded; webbing thick, leaving half of terminal phalanges of first three toes free; fourth toe with 2 to 2½ phalanges free, fifth toe with one phalanx free; subarticular and metatarsal tubercles obscure or absent; tibia 0.34–0.41 of snout-vent.

Dorsum with scattered small conical tubercles; tubercles forming irregular dorsolateral rows;[1] sides and ventral surfaces coarsely granular.

Color (in alcohol) yellowish brown above, darker on sides; the lighter mid-dorsal area sometimes with two or three dark spots; throat yellow with brown spots or brown with yellow spots; similar pattern on pectoral and abdominal regions, except that brown areas usually more extensive. In life, "black; ventral tubercles white; sometimes marbled with large white blotches" (Smith, 1931A).

Secondary sex characters.—As Table 12 indicates, females are about the same size as males. Tympanum diameter, expressed as thousandths of snout-vent length, ranges from 59 to 79 (median 69) in

[1] These rows are not as conspicuous as drawn in the illustration accompanying the original descripton.

seven females and from 56 to 74 (median 66) in six males. Comparing the sexes by means of the Mann-Whitney U test (Siegel, 1956) shows the differences in relative tympanum diameter to be insignificant statistically ($P > 0.12$).

Males have a median subgular vocal sac having single or paired slit-like openings into the mouth. Males also have a single row of yellow or brown spinules under the mandible and a yellow or brown nuptial pad on the first finger. The color of the mandibular spines and nuptial pads agrees with the color of the surrounding skin. Minute spinules, many of them tipped with melanin, are distributed over the entire dorsum in males only.

Ecological notes.—Specimens of *misera* have been caught in the mossy, montane forest of Kina Balu. Of the specimens examined 13 were caught at 2200 meters and 13 at 3000. Assuming the correctness of the identification, Smith (1925A) reported *misera* from near 2000 meters.

Range.—Reported from Sabah and northern Sarawak.

SABAH: Kota Belud District, Kamborangah and Pakka on Mount Kina Balu. SARAWAK: Fifth Division, Mount Murud (Smith, 1925A).

Pedostibes Günther

These species have a movable coccyx, eight presacral vertebrae, a complete quadratojugal, and numerous small pigmented ova. The ecology and behavior of only one species, *hosei*, are known to any extent (p. 96). But as the ova are similar in two others and as all species have expanded finger tips, it is likely that all are at least partly arboreal as adults and live in pools of small forest streams as larvae.

KEY TO BORNEAN SPECIES (Fig. 20).

1A. Tarsal ridge present (fig. 20A) .... 2.
B. No tarsal ridge .... 3.

2A. Parotoid oval or circular (fig. 20C), lateral and medial borders convex *rugosus.*
B. Parotoid triangular (fig. 20B), lateral border straight or concave, medial border convex .... *hosei.*

3A. Parotoid gland present; tympanum visible .... *everetti.*
B. No parotoid gland; tympanum absent .... *maculatus.*

Pedostibes everetti (Boulenger)

Nectophryne everetti Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 450—Mount Kina Balu, Sabah; Roux, 1906, Proc. Zool. Soc. London, **1906**,

p. 61, pl. 2, fig. 2 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 68; Smith, 1925, Sarawak Mus. Jour., **3**, p. 31; 1931, Bull. Raffles Mus., no. 5, p. 30.

Pedostibes everetti Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 192.

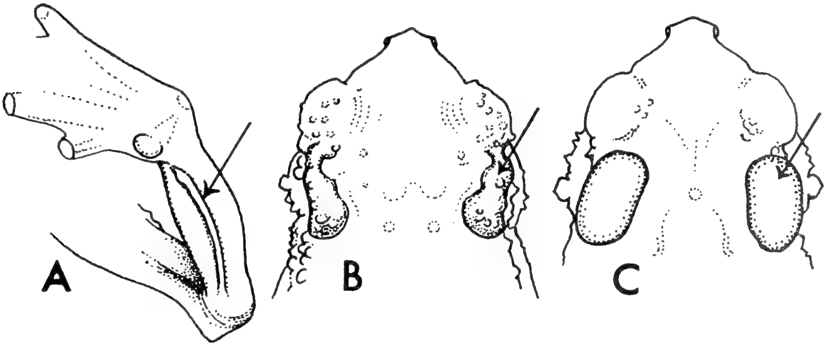


FIG. 20. Key to species of *Pedostibes*.

Material examined.—Borneo 1 (BM, holotype).

Taxonomic notes.—The British Museum specimen from Penrissen, Sarawak placed in this species by Roux (1906) is generically distinct from *everetti*. The Sarawak specimen is an adult female (and not a male, as Roux said) containing enlarged (1.6 mm.), non-pigmented ova. Its webbing is less extensive (not reaching disks of third and fifth toes) than that of *everetti*, the tips of the fingers are wider (wider than tympanum) than those of *everetti*, and it lacks a parotoid.

Pedostibes everetti is very similar to *P. rugosus*, the main differences being the absence of a tarsal ridge, the smaller digital disks, and the greater separation of parotoid and eyelid in *everetti*. The holotype of *everetti* may be a juvenile. Only 33.0 mm., it is a male (according to my dissection; a female according to the original description) lacking vocal sacs and nuptial pads. Five juveniles (21.4–33.2 mm.) of *rugosus* suggest ontogenetic variation in the size and position of the parotoid (see also *hosei*, p. 95). In a 28.8 mm. specimen of *rugosus*, the parotoid is separated from the eyelid about the same amount as in the holotype of *everetti*. In two slightly larger *rugosus* (32.4, 33.2 mm.) the parotoid is separated from the eyelid by about half the width of the gland, in other words, by a much shorter gap than in *everetti*. Thus, even allowing for ontogenetic change in position of the gland, this difference between these species remains. All five juveniles of *rugosus* have tarsal ridges and wider terminal phalanges than *everetti*.

Description.—Body moderately stout; no cranial crests; tympanum distinct, one-third eye diameter; parotoid oval, length subequal to diameter of eye, separated from eyelid by slightly less than its own width; dorsum with scattered small spinose tubercles.

Fingers long, tips dilated into small truncate disks, disks much smaller than tympanum; first finger much shorter than second; fingers webbed at bases. Tips of toes feebly dilated; first three toes webbed to disks on outer edges, fifth toe to disk on inner edge, fourth toe with two phalanges free; two metatarsal tubercles; no tarsal ridge.

Color (in alcohol) gray above with large reddish brown spots over all dorsal and lateral surfaces; lips and cheek with bold reddish bars; below immaculate, cream-colored.

Range.—Known only from Mount Kina Balu, Sabah.

Pedostibes maculatus (Mocquard)

Nectophryne maculata Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 162, pl. 11, fig. 8—Mount Kina Balu, Sabah; Roux, 1906, Proc. Zool. Soc. London, **1906**, p. 63; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 71; Smith, 1931, Bull. Raffles Mus., no. 5, p. 30.

Pelophryne maculata Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 193.

Material examined.—Borneo 6 (3 MHNP, types of *maculatus*; 2 NHMW; 1 ZMB).

Taxonomic notes.—Barbour (1938) gave no explicit reasons for placing *maculatus* Mocquard in the genus *Pelophryne* though we may assume that he believed it had seven presacral vertebrae and a coccyx expanded dorsally and fused to the sacrum. In the three non-typic specimens, which were compared with the types, the coccyx is not expanded dorsally and is not fused to the sacrum. An X-ray negative of one specimen shows it to have eight presacral vertebrae.

The ova of two syntypes of *maculatus* (MHNP 89.266–67) are small and numerous (more than 50 per ovary). True *Pelophryne* (see pp. 55, 78) have huge ova relative to body size (cf., Inger, 1960A) and probably rarely more than 10 per ovary (pp. 79, 87). Thus, *maculatus* differs from the diagnosis of *Pelophryne*.

On the other hand, its small ova, complete quadratojugal, and arciferal girdle clearly ally *maculatus* with *Pedostibes hosei* and *P. rugosus*.

Description.—A small *Pedostibes*, adult males about 40 mm., females 45–50; habitus slender, limbs long; head without bony crests; head width 0.27–0.30 of snout-vent; snout truncate, projecting in

profile; no tympanic annulus or eustachian tubes; dorsal and lateral surfaces with numerous small, round warts bearing minute blackish spines; no parotoid gland.

Fingers long, terminal phalanges expanded into truncate disks, those of outer fingers about one-third diameter of eye; first finger much shorter than second; subarticular tubercles moderate; web reaching basal subarticular tubercles but not extending distally as a fringe. Tips of toes blunt, not expanded; webbing extensive, first two toes with one phalanx free, third toe with 1 to 1½ free, fourth with three, and fifth with one to 1⅔ free; an oval inner and a conspicuous round outer metatarsal tubercle; no tarsal ridge; tibia 0.54–0.60 of snout-vent length.

Color (in alcohol) grayish brown above; irregular dark spots dorsally and laterally; limbs with dark crossbars; below grayish.

Secondary sex characters.—The single male examined (ZMB 29466) has no vocal sac openings or mandibular spines. A blackish nuptial pad covers the dorsal surface of the first finger from the distal third of the metacarpal to the end of the basal phalanx and the medial edge of the entire metacarpal.

Four adult females, the smallest and largest containing enlarged ova, measure 45.0–50.8 mm., compared to 41.7 for the adult male.

Range.—Known only from Mount Kina Balu and "North Borneo."

Pedostibes hosei Boulenger

Nectophryne hosii Boulenger, 1892, Proc. Zool. Soc. London, **1892**, p. 508, pl. 30, fig. 2—Mount Dulit, Sarawak.

Pedostibes hosii Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 192.

Material examined.—Borneo 226 (1 AMNH; 1 BM, type; 198 FMNH; 1 MCZ; 4 NSH; 7 RMNH; 14 SM); Sumatra 2 (MCZ); Thailand 4 (MCZ).

Description.—Body moderately stout; no bony cranial crests; tympanum distinct, about half eye diameter; parotoid gland conspicuous, triangular, about as long as eye, separated from eye by narrow glandular ridge; back, sides, and top of legs with small round warts; area between parotoids smooth or with a pair of warts.

Fingers long, expanded at tips into truncate disks; web reaching basal subarticular tubercles or slightly beyond and extending to disks as narrow fringe. Tips of toes round, swollen; first three toes webbed to disks on lateral borders, fifth toe to disk on inner edge, fourth toe to middle subarticular tubercle or slightly beyond; an oval inner

metatarsal tubercle and tarsal tubercle and a smaller, rounder outer one; a sharp tarsal ridge; tibia 0.43–0.49 of snout-vent.

Color (in life) of adult males immaculate brown or blackish above, dirty whitish or yellowish below; adult females above purplish with yellow vermiculation (7 specimens) or uniform brown (2); lips barred.

Secondary sex characters.—In addition to the sex dimorphism in coloration described above, the sexes differ in size, the females being much larger. The nine females examined measure 88.5 to 104.8 mm. (mean 97.42). Mature Bornean males seen have a snout-vent range of 52.9–79.6 (mean 64.86 ± 1.08 mm.; N = 34).

All of these males have median, subgular vocal sacs reaching both mandibles and having a single, slit-like opening into the mouth. In addition all males have a nuptial pad consisting of a cluster of small blackish brown asperities on the dorso-median surface of the first finger from about the center of the metacarpal to the base of the terminal phalanx.

Males also have small whitish or dark spinules, usually appearing as tips of warts, on the back, the upper eyelid, and the dorsal surfaces of the hind limbs.

Larvae and juveniles.—Two series of larvae, collected in central Sarawak and Sabah in streams along which *hosei* males were calling, are in hind limb bud Stages IV (length of limb bud 1½ times its diameter) to XI (all toes distinct). Additional tadpoles, two in Stage XVII, were obtained from northern Sarawak. The sinistral spiracle, median vent, and laterally restricted papillae confirm the family identification while the rather generalized oral disk limits generic identification to *Bufo* and *Pedostibes.* The hand of the most advanced tadpole has fully developed fingers; the first finger is distinctly shorter than the second, which is half as long as the third. In the forest-inhabiting species of *Bufo,* the first finger is equal to or longer than the second. Advanced tadpoles of *Bufo biporcatus,* which are very similar to these, have the first two fingers subequal and the second less than half the length of the third. In *Pedostibes hosei* and *P. rugosus* the first finger is shorter than the second, and the second is at least half the length of the third. Since only the former was observed at these two localities, it is probable that the larvae are those of *hosei.* A description of the larvae (fig. 21) follows.

Body broadly oval, depressed, flat below, head and body 5.9–8.1 mm.; eyes dorsal, closer to one another than to tip of head; nostrils large, closer to eye than to tip of head, separated from each other by little more than eye diameter; oral disk ventral, subterminal, half

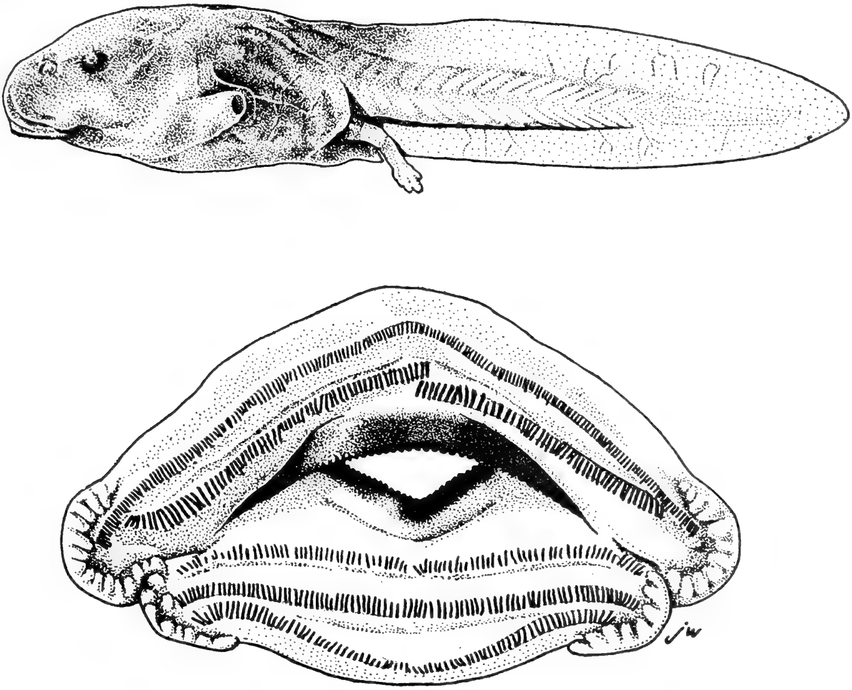


FIG. 21. Tadpole of *Pedostibes hosei*. Lateral view above (× 7). Oral disk below (× 40).

maximum width of body; papillae short, in several rows, confined to lateral quarters of lips; labial teeth I:1+1/III (22), II/III (7); inner upper tooth row narrowly interrupted, three lower rows subequal in length; spiracle sinistral, low on side, mid-way between tip of snout and end of body; gut tightly coiled; tail bluntly rounded, 0.53–0.58 of total length; fins subequal, deeper than tail muscle; total lengths at Stages X–XI 15.2–19.3 mm.

Body brown above, without pigment below; tail muscle brown; fins colorless.

Newly transformed young measure 8.2–10.5 mm. Dorsally they are blackish-brown with black areas enclosing small red spots. Ventrally they are lighter. The dorsal surfaces of the limbs are barred. The subarticular tubercles and the metatarsal tubercles are red. At this size the parotoids are not present and the tips of the fingers are not expanded. The parotoids begin to develop when the toads reach about 12 mm. and the disks at about 13 or 14 mm. A juvenile was previously misidentified as *Ansonia* (Inger, 1956).

Ecological notes.—Previous papers (Boulenger, 1912; Smith, 1930) report *hosei* as being caught in bushes and small trees in dense forest. My own observations are that males usually call from low vegetation (up to a height of about two meters) along small streams but may also call from the banks.

Newly transformed toads are often encountered on the banks of small forest streams having slow to moderate currents. From there they forage widely on the forest floor. They are commonly seen even on hills as much as 100–200 meters above the beds of their natal streams; juveniles as small as 11 mm. (FMNH 139361) and as large as 34 mm. (FMNH 138108–9) have been found in such situations.

Eleven of 161 toads were caught in secondary growth, the remainder in primary rain forest. None of these specimens was collected more than 300 meters above sea level.

Data available are not adequate to define the reproductive cycle. However, the collection of 99 newly transformed young in June and series of young larvae (see above) in June and August demonstrate that breeding takes place at least in the interval May-August.

Range.—From the northern end of peninsular Thailand to Sumatra and Borneo.

SABAH: Kinabatangan District, Deramakot, southeast end of Dewhurst Bay; Lahad Datu District, Sungei Pangaruan; Tawau District, Kalabakan. SARAWAK: First Division, Kuching, Pangkalan Ampat, Samunsam; Second Division, Lupar River valley; Third Division, Baleh River near mouth of Putai River, Mengiong River, Mount Dulit; Fourth Division, Long Bareh, Long Akah, Niah, Sungei Melana, Siniei. KALIMANTAN: Long Petah, upper Mahakam valley, Sintang, Sungei Landak.

Pedostibes rugosus Inger

Pedostibes rugosus Inger, 1958, Sarawak Mus. Jour., **8**, p. 476, fig. 1—Sungei Menuang, Third Division, Sarawak.

Material examined.—Borneo 10 (1 FMNH, holotype; 8 RMNH; 1 SM, paratype).

Description.—Body stout; no cranial crests; tympanum distinct, less than one-half eye diameter; conspicuous oval parotoid gland separated from eyelid by about half width of parotoid; back, upper eyelids, and dorsal surfaces of limbs with numerous round warts, all smaller than tympanum; area between parotoids with many small warts.

Fingers long, tips dilated into truncate disks; disks equal to or wider than tympanum; first finger much shorter than second; subarticular tubercles distinct; web reaching subarticular tubercle of first finger, beyond basal subarticular tubercle on outer edge of second and third fingers and inner edge of fourth. Tips of toes round, swollen; first three toes webbed to disks on outer edges, fifth toe to disk on inner edge, fourth toe to base of distal subarticular tubercle (i.e., two phalanges free); a flat oval inner metatarsal tubercle; a flat roundish outer metatarsal tubercle; a sharp tarsal ridge.

Color (in alcohol) bluish gray or brown above and on sides; back with many dark brown spots and short stripes; top and sides of head with broad, dark brown bars; dorsal surfaces of limbs crossbarred; all ventral surfaces immaculate cream-colored.

Secondary sex characters.—Three females with enlarged, pigmented ova measure 80–95 mm., two adult males 74.3 and 76.8 mm.

Males have median, subgular vocal sacs with a single, slit-like opening. The dark brown or black nuptial pad covers the entire dorsal and medial surface of the first finger from the palmar tubercle to the center of the terminal phalanx and a narrow medial strip of the second finger.

The dorsal and lateral warts of both sexes are studded with small black spines which are usually larger and more numerous in the males.

Ecological notes.—This species has been collected only in primary forest at low to moderate elevations, the holotype at approximately 525 meters, the paratype at 1000 meters, and one specimen in the lowlands of the Kapuas valley.

Range.—Known only from central and western Borneo.

SARAWAK: First Division, Mount Penrissen; Third Division, Sungei Menuang in headwaters of Baleh River. KALIMANTAN: upper Mahakam valley, Sintang.

Ansonia Stoliczka

Only abbreviated descriptive notes of the species covered in the recent review (Inger, 1960B) will be presented here. Since publication of the revision, additional specimens of four of those species have come to light.

Three species are added to the genus: *Bufo fuligineus* Mocquard and two new species, *latidisca* and *guibei*, described below. A revised key to the genus, accommodating these additional forms, follows (fig. 22).

1A. Tympanum not visible externally .... 15.
B. Tympanum visible externally .... 2.

2A. First finger not reaching disk of second when fingers are adpressed (fig. 22A) .... 3.
B. First finger reaching disk of second (fig. 22B) .... 11.

3A. Sharp tarsal ridge present (fig. 22C) .... 4.
B. No tarsal ridge .... 5.

4A. A white spot below eye; a whitish band from eye to arm (fig. 22D) *albomaculata.*
B. Without above pattern .... *minuta.*

5A. Abdomen with large yellow areas (fig. 22E) .... 6.
B. Abdomen without large yellow areas .... 7.

6A. Upper lip barred with yellow .... *malayana.*
B. Upper lip uniformly dark .... *ornata.*

7A. Tips of outer fingers dilated into spatulate disks distinctly wider than basal phalanges (fig. 22F) .... 8.
B. Tips of outer fingers rounded .... 10.

8A. Disk of third finger subequal to diameter of tympanum .. *latidisca* new species.
B. Disk of third finger much narrower than tympanum .... 9.

9A. Distance between tympanum and mouth half or less than half of the distance between nostril and mouth .... *platysoma.*
B. Distance between tympanum and mouth more than half of the distance between nostril and mouth .... *hanitschi.*

10A. Snout projecting beyond mouth in profile (fig. 22G) .... *malayana.*
B. Snout vertical in profile, not projecting (fig. 22H) .... *fuliginea.*

11A. At least two phalanges of third and fifth toes free of web (fig. 22I) .. *leptopus.*
B. Less than two phalanges of third and fifth toes free of web (fig. 23J) .... 12.

12A. An oblique flap of skin on each side of vent .... *guibei* new species.
B. No such flap of skin .... 13.

13A. Abdomen dark with light spots .... *penangensis.*
B. Abdomen light with dark spots or with light and dark spots of equal area .. 14.

14A. A pair of longitudinal ridges or rows of tubercles between eyes (fig. 22K) *longidigita longidigita*
B. No such ridges or rows of tubercles .... *longidigita gryllivoca.*

15A. Males with vocal sacs less than 31 mm.; females with convoluted oviducts less than 38 mm. .... *muelleri.*
B. Males with vocal sacs more than 31 mm.; females with convoluted oviducts more than 40 mm. .... *mcgregori.*

Ansonia albomaculata Inger

Ansonia albomaculata Inger, 1960, Fieldiana, Zool., **39**, p. 489, figs. 82A, 87, 88B—headwaters of Baleh River, Sarawak.

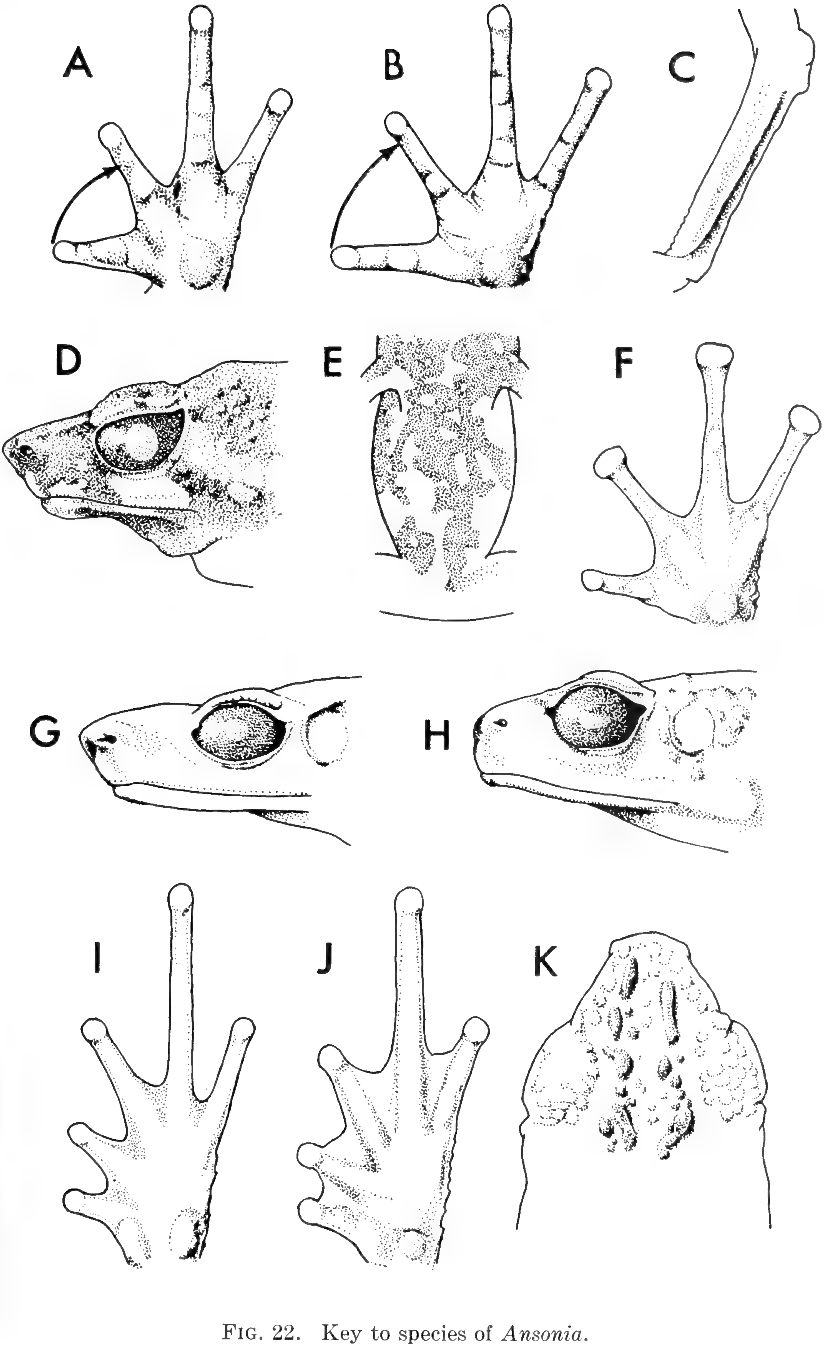


FIG. 22. Key to species of *Ansonia*.

Material examined.—Borneo 48 (29 FMNH, including holotype and paratypes; 1 RMNH; 18 SM, paratypes).

Descriptive notes.—A small species, males 20–25 mm.: finger tips rounded; tip of first finger not reaching disk of second when fingers are adpressed; third and fifth toes webbed to disks in males; a sharp tarsal ridge; no interorbital ridges; a white spot below eye; a light band from eye to arm.

Color (in life) of dorsal surfaces dark brown; edge of eyelid red; side of head with dark red spots; scattered dorsolateral warts red; throat dark brown with faint yellow spots; chest and belly yellow-green with large black blotches anteriorly; upper arm and anterior face of thigh with orange spots; hind limb with narrow orange-red cross bars; yellow spot at elbow and heel.

Secondary sex characters.—Males have subgular vocal sacs with single, elongate openings which may be on the left or right. A yellowish nuptial pad on the dorsal surface of the first finger covers half of the metacarpal and the basal phalanx. The underside of the mandible lacks spines.

The three females seen are much larger than the males and measure 33.6–33.8 mm.

Larvae.—Body oval, depressed; eye dorso-lateral; spiracle sinistral, low on side; vent median; tail margins subparallel, tip blunt; caudal muscle deeper than fins in proximal half.

Oral disk as wide as body; lips expanded; upper lip with single row of short papillae laterally; lower lip with a single continuous row of short papillae; labial teeth II/III; upper beak divided, lower single.

Ecological notes.—All adults collected so far have been obtained in rain forest below 518 meters (1700 feet) above sea level. Both juveniles and adults (total 6) have been found under leaves and logs on the forest floor by day. One adult when caught was sitting on a leaf 18 cm. above ground beside a small, slow, forest stream. Calling males (7) and pairs in amplexus (2) were found only on the banks of large streams (ca. 10–50 m. wide). The tadpoles have typical swift-water adaptations and the three known were caught in a small, rocky stream.

Range.—Western Borneo.

SABAH: Ranau District, Sungei Kepungit. SARAWAK: Second Division, Lupar River valley; Third Division, Mengiong River, headwaters of Baleh River; Fourth Division, Long Sinei and Meligong on the Akah River, Sungei Patah. KALIMANTAN: upper Sibau River.

Ansonia minuta Inger

Ansonia minuta Inger, 1960, Fieldiana, Zool., **39**, p. 493, figs. 81A, 89, 90—Matang, Sarawak.

Nectophryne signata (not of Boulenger) Smith, 1925, Sarawak Mus. Jour., **3**, p. 31.

Material examined.—Borneo 43+larvae (1 BM; 27+larvae FMNH; 1 MCG; 1 MHNP; 1 RMNH; 11 SM; 1 ZMB).

Taxonomic notes.—One (MHNP 8129) of the Penrissen specimens identified by Smith (1925B) as *Bufo* (=*Cacophryne*) *borbonica* has all of the characteristics of *A. minuta.* In particular, it has broadly overlapping epicoracoids, which immediately differentiate it from species of *Cacophryne.* The webbing, tarsal ridge, and coloration are like *minuta.*

The series identified by Smith (1925B, p. 31) as *N. signata* does not differ in any significant way from *Ansonia minuta.* The largest specimen, a female with enlarged ova, is 28 mm. and not 38 as stated by Smith.

Descriptive notes.—A small species (males 20–25 mm., females to 28 mm.); tips of outer fingers spatulate; tip of first finger not reaching disk of second when fingers are adpressed; third and fifth toes with at most two phalanges free of web (see *Secondary sex characters*); a sharp tarsal ridge; no interorbital ridges; no white band from eye to arm.

Secondary sex characters.—Females (mean 24.39 ± 0.29 mm.; N = 12) are larger than males (mean 22.14 ± 0.19 mm.; N = 14). The third and fifth toes of females have one to two phalanges free of web, whereas in males those toes are webbed to the disks. Males have two to four rows of spinose tubercles under the mandibles and median subgular vocal sacs that open by single slits that may be on either side of the mouth. Nuptial pads were not visible on any of the 16 adult males seen.

Larvae.—Body form like that of larval *albomaculata*; oral disk as wide as body; lips expanded; lower lip with a complete marginal row of short papillae and one complete and one interrupted row of short, thick inframarginal papillae; marginal papillae extend onto corners of upper lip; labial teeth II/III; upper beak divided, halves widely separated; lower beak single.

Ecological notes.—Twenty-seven of the known specimens were collected on rocks and low herbs beside a small stream flowing though primary rain forest on the slopes of Mount Matang at about 100 me-

ters above sea level. Numerous larvae were seen (and collected) clinging to the rocky substrate in the full force of the current. They could be dislodged only by shoving a stiff-edged leaf or a knife between their oral disks and the substrate. Specimens have also been collected at 610 meters above sea level.

Five of 12 females collected late in July contained enlarged (ca. 2.0 mm.), non-pigmented ova. One female (24.6 mm.) had 47 enlarged ova (1.8–2.0 mm.) and about half that number of very small ova (0.5 mm.) in the left ovary. As males were calling and young larvae were found at the same time, breeding activity was occurring then.

Range.—Known only from western Borneo.

SARAWAK: First Division, Bungar Range, Matang, Mount Penrissen. KALIMANTAN: Mount Simedum, Sambas.

Ansonia platysoma Inger

Ansonia platysoma Inger, 1960, Fieldiana, Zool., **39**, p. 487, fig. 86—Luidan River, Bundu Tuhan, Sabah.

Material examined.—Borneo 7, type series (5 FMNH; 1 MCZ; 1 NHMW).

Descriptive notes.—A small species (both sexes 20–25 mm.); tips of outer fingers spatulate; tip of first finger not reaching disk of second when fingers are adpressed; third toe usually webbed to disk in males, fifth toe usually with one compete phalanx free; females with slightly less webbing; no tarsal ridge; no light band from eye to arm.

Secondary sex characters.—The only mature female (24.3 mm.) seen is slightly larger than mature males (21.5–22.8 mm.). The vocal sac in three males is like that of male *albomaculata*. Mandibular spinose tubercles are lacking. A blackish brown nuptial pad is present on the dorsal and medial surfaces of the metacarpal and basal phalanx of the first finger.

Ecological notes.—The only definite locality for this species is at 1000 meters above sea level.

Range.—Known only from Bundu Tuhan on the slopes of Mount Kina Balu, Sabah.

Ansonia fuliginea (Mocquard)

Bufo fuligineus Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **2**, p. 158, pl. 11, fig. 5—North Borneo; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 77.

Nectophryne altitudinis Smith, 1931, Bull. Raffles Mus., no. 5, p. 14, pl. 1, fig. 1 —Pakka, Mount Kina Balu, Sabah.

Pedostibes altitudinis Barbour, 1938, Proc. Biol. Soc. Washington, **51**, p. 192.

Material examined.—Borneo 16 (5 BM, holotype and paratypes of *N. altitudinis*; 5 FMNH, 1 paratype of *N. altitudinis*; 1 MHNP, holotype of *B. fuligineus*; 3 SNM, paratypes of *N. altitudinis*; 1 Univ. of Malaya).

Taxonomic notes.—The external morphology of the holotype of *B. fuligineus* agrees point for point with the types and topotypes of *N. altitudinis*, allowing for sex dimorphism of the fore limb.

Generic allocation has been a problem partly because the unique holotype of *fuliginea* could not be dissected and partly because Barbour (1938) had access only to an X-ray photograph of *altitudinis*. Barbour placed *altitudinis* in the genus *Pedostibes* solely on the basis of the presacral vertebral count (8) and the movable coccyx. These characters, though they do serve to distinguish *Pedostibes* from *Pelophryne*, which was Barbour's purpose, do not separate *Pedostibes* from *Ansonia* (Tihen, 1960).

This species has characters that clearly associate it with *Ansonia* and prohibit allocation to *Pedostibes* or *Bufo*. These characters are: (1) a strong, transverse parasphenoidal ridge, (2) an incomplete quadratojugal, and (3) large, non-pigmented ova that are relatively few in number (less than 100 per ovary). It also differs from *Bufo* in lacking parotoids and in having weak subarticular tubercles.

Description.—A moderate-sized species, adult females 38–44 mm., males 32–36 mm.; habitus moderately stocky; head width and length subequal; snout subequal to eye, rounded, vertical in profile; nostril above symphysis; canthus sharp; lores oblique, weakly concave; interorbital about 1½ times width of upper eyelid; tympanum distinct, about half diameter of eye.

Tips of fingers slightly swollen, but not forming disks; tip of first finger not reaching base of swollen tip of second; first two fingers webbed to subarticular tubercles; subarticular tubercles feebly distinct. Tips of toes like those of fingers; web leaving one to two (usually less than two) phalanges of third and fifth toes and three phalanges of fourth toe free; no tarsal ridge; a weak outer metatarsal tubercle.

Skin above and on sides with low, round warts, those on sides sometimes bearing numerous melanic spinules; no interorbital ridges or rows of tubercles; ventral surfaces coarsely granular.

Color (after Smith, 1931A) brownish in vertebral region; blackish on sides and below; abdomen with or without small yellow spots; limbs yellowish brown below.

Secondary sex characters.—Seven females containing enlarged, non-pigmented ova (2.0–2.8 mm.) measure 39.5–42.2 mm. The left ovary of one female had 51 enlarged ova.

The holotype (35.6 mm.) is the only fully mature male I have seen. It has a slit-like vocal sac opening on the right side of the mouth. The nuptial pad consists of 26 separated, large, black spines on the first finger and 10 smaller ones on the second finger. The mandible has a double row of black spinules as in other species of *Ansonia*. A smaller (32.0 mm.), subadult male (FMNH 152175) lacks a vocal sac opening and mandibular spinules. It does have separated spines on the first and second fingers, but they lack melanin.

Ecological notes.—Fourteen specimens with precise data have been collected between 1800 and 3000 meters above sea level.

Range.—Known only from western Sabah.

SABAH: Ranau District, Kamborangah, Mentaki Ridge, Pakka—all on Mount Kina Balu.

Ansonia guibei[1] new species

Holotype.—Field Museum of Natural History 152159, an adult male from Mesilau Cave camp, 1800 m., Mount Kina Balu, Sabah. Collected 6 April 1964, by Lord Medway.

Diagnosis.—A moderate-sized species, males ca. 32 mm.; tympanum visible externally; tips of fingers not expanded; first finger reaching base of tip of second; no interorbital ridges; no tarsal ridge; an oblique flap of skin on each side of vent.

Description of holotype.—Habitus slender, limbs long; head as wide as long; snout subequal to eye, obtusely pointed, vertical in profile; nostril above symphysis; canthus rostralis sharp; lores sloping, weakly concave; interorbital much wider than upper eyelid; tympanum distinct, one-fourth to one-third diameter of eye.

Fingers slender, longer; tips swollen but not expanded into disks; first finger reaching base of tip of second; first finger measured from median edge of palmar tubercle longer than diameter of eye; fourth and second fingers equal; subarticular tubercles weak; a large, round palmar tubercle.

[1] Named in honor of Dr. Jean Guibé, Museum National d'Histoire Naturelle, for his particular help with material of this genus.

Tips of toes like those of fingers; third and fifth toes equal in length; membranous web reaching tips of first, second, third, and fifth, 2½ phalanges of fourth toe free; subarticular tubercles weak; an oval, inner and a smaller, round outer metatarsal tubercle; no tarsal ridge.

Skin dorsally and dorsolaterally with numerous round warts topped with clusters of dark spinules; sides and ventrum with coarse granules; parotoid region with warts; no crests or rows of tubercles on head; a flap of skin on each thigh beginning at the vent and extending laterally and ventrally.

Color (in alcohol) blackish brown above with light spots outlining an indistinct dark pattern; dorsal surface of hind limb with light spots; ventrally whitish with brown suffusion on throat and spots on chest.

Measurements given below.

Paratype.—FMNH 152160; an adult male from type locality.

This specimen agrees with the holotype in all of the characters mentioned above. Measurements (mm.) of the two specimens follow:

	Holotype	Paratype
Snout-vent	32.0	32.1
Head width	10.3	10.0
Head length	10.2	10.0
Tibia	14.6	14.2

Secondary sex characters.—Neither male has a vocal sac opening though both have fully developed nuptial pads and must be considered mature. The nuptial pad consists of a cluster of several hundred spinules covering the dorsal and median surfaces of the first finger and a similar, though smaller cluster on the dorsomedial edge of the second finger. The median edge of the third finger bears a row of similar spinules. The mandible has a staggered row of black spinules.

Comparisons.—*Ansonia guibei* is the only species of the genus in which adult males lack vocal sacs. It is also the only known species of *Ansonia* having oblique flaps of skin adjacent to the vent. *Ansonia guibei* further differs from the larger species (i.e., males at least 30 mm.) in the following ways: from *latidisca* in lacking expanded finger tips; from *fuliginea* in the form of the nuptial pad and in having the third and fifth toes completely webbed; from *leptopus* in having fully webbed toes; from *longidigita* in lacking interorbital ridges or rows of tubercles; and from *muelleri* and *mcgregori* in having an exposed tympanum and in lacking a tarsal ridge.

With the possible exception of *penangensis*, the remaining species of *Ansonia* are smaller than *guibei* and differ from it in having shorter first fingers (*malayana, ornata, platysoma*) or tarsal ridges (*albomaculata, minuta, hanitschi*) as well as in the characters previously mentioned.

The relationship between *A. guibei* and *penangensis* is not clear because I have seen only males of the former and only females of the latter. In contrast to *guibei, penangensis* has 1½ phalanges of the third and fifth toes free of web and no flaps of skin adjacent to the vent. If these characters show sexual dimorphism in these forms, as extent of webbing does in some species (e.g., *A. malayana, A. albomaculata*), they may be very closely related.

Range.—Known only from the type locality on Mount Kina Balu, Sabah.

Ansonia hanitschi Inger

Ansonia hanitschi Inger, 1960, Fieldiana, Zool., **39**, p. 484, fig. 85—Mount Kina Balu, Sabah.

Bufo leptopus (not of Günther) Smith, 1931, Bull. Raffles Mus., no. 5, p. 13 (part).

Material examined.—Borneo 14 (10 BM, holotype and paratypes; 2 FMNH, paratypes; 1 MCZ, paratype; 1 NMB).

Descriptive notes.—A medium-sized *Ansonia*, males 23–27, females 29–32 mm.; tips of outer fingers spatulate; tip of first finger not reaching disk of second when fingers are adpressed; third and fifth toes with 1½ to 2 phalanges free of web in both sexes; no tarsal ridge; no light band from eye to arm.

Secondary sex characters.—All nine females (29.5–31.9 mm., mean 30.96) are larger than the four adult males seen (26.1–26.3 mm.). One male lacking vocal sacs measures 23.3 mm. *Ansonia hanitschi* has only slight sex dimorphism in the extent of webbing. Adult males have 1 to 1½ (modal value 1½) phalanges of the third toe free of web and females one to two (modal value 2).

The vocal sac resembles that of *A. albomaculata.* Males have one or two rows of yellowish spinose tubercles under the mandible. A dark brown nuptial pad covers the dorsal surfaces of the metacarpal and basal phalanx of the first finger.

Ecological notes.—Specimens have been collected at 1275 (2 specimens) and 1675 (6) meters above sea level on Mount Kina Balu.

Range.—Known only from the Kadamaian (Tempasuk) River and Lumu Lumu on Mount Kina Balu, Sabah.

FIG. 23. *Ansonia latidisca*, new species.

Ansonia latidisca new species. Figure 23.

Holotype.—Rijksmuseum van Natuurlijke Historie, Leyden, 10677; an adult male from top of Mount Damus, Sambas, Kalimantan. Collected by Dr. J. G. Hallier.

Diagnosis.—A large species (adult males about 35 mm., females about 55 mm.); tympanum visible externally; tips of fingers dilated into truncate disks, that of third as wide as tympanum; tip of first finger not reaching disk of second; two rows of interorbital, conical tubercles; no tarsal ridge.

Description of holotype.—Habitus slender; limbs long; head slightly longer than broad; snout subequal to eye, truncate, constricted before eyes, almost vertical in profile; nostril above symphysis; canthus rostralis sharp; lores vertical, weakly concave; interorbital at narrowest part equal to width of upper eyelid; tympanum distinct, about one-third diameter of eye.

Fingers slender, long; tips of three outer fingers dilated into truncate disks about twice width of basal phalanges; disk of third finger as wide as tympanum; first finger not reaching base of disk of second; first finger (measured from median edge of palmar tubercle) equal to diameter of eye; fourth finger longer than second; subarticular tubercles feebly distinct; a large, round palmar tubercle laterally; fingers with distinct web basally, web reaching subarticular tubercles of first two fingers.

Tips of toes swollen but not forming truncate disks, much narrower than tips of fingers; third and fifth toes of equal length; membranous web reaching base of disks on first two toes, leaving two phalanges of third and fifth toes and 3½ of fourth toe free; subarticular tubercles obscure; an oval inner and a smaller, round outer metatarsal tubercle; no tarsal ridge.

Skin above and laterally covered with large and small conical tubercles; no parotoids; two rows of large conical tubercles beginning on snout and extending back to occiput; ventral surfaces coarsely granular.

Color (in alcohol) above and on sides light brown with numerous, irregular reddish brown spots; below brown with scattered, small yellowish spots posteriorly.

Measurements in Table 13.

Paratype BM 99.12.8.12; an adult female from Mount Penrissen, First Division, Sarawak.

TABLE 13.—Measurements (mm.) of holotype (male) and paratype (female) of *Ansonia latidisca* new species.

	Holotype	Paratype
Snout-vent	34.9	54.0
Head length	11.4	15.4
Head width	10.8	14.9
Tibia	19.2	24.7
Tympanum diameter	1.5	3.2

Except for size (Table 13) and other secondary sex characters (see below), this specimen agrees remarkably well with the holotype. The spinose dorsal tuberculation shows some variation, but both specimens have the larger tubercles in the same positions: two interorbital rows, a vertebral row or pair of rows, and a dorso-lateral row.

The ventral color of the paratype is lighter (a brownish yellow or cream-color) than that of the holotype.

The non-pigmented ova of the paratype measure 1.5–1.8 mm.

Secondary sex characters.—The male holotype, besides being smaller, has a darker throat than the female paratype. The male also has three or four rows of small, melanin-tipped spines on the lower jaw. The slit-like vocal sac opening is on the left side. Nuptial pads are not visible.

Ecological notes.—*Ansonia latidisca* is evidently another montane species, living at elevations comparable to *A. hanitschi* and *A. platysoma*. The holotype was collected at about 1200 meters. Though no altitude was given for the paratype, it came from Mount Penrissen, which reaches 1300 meters.

Comparisons.—*Ansonia latidisca* has wider disks on the fingers than any other species in the genus; hence the specific name. It is the only *Ansonia* in which the disk of the third finger is as wide as the tympanum. The large species, *leptopus* and *longidigita,* further differ from *latidisca* in having a relatively longer first finger (reaching base of disk of second). *Ansonia mcgregori,* the third species comparable in size to *latidisca,* has the tympanum invisible externally.

The remaining species are all smaller (adult females under 40 mm., males under 30 mm.) than *latidisca.* Two of them, *minuta* and *albomaculata,* differ from *latidisca* in having a distinct tarsal ridge. Another, *penangensis,* has a relatively long first finger (as in *leptopus,* see above). Another, *muelleri,* has no externally visible tympanum and has more extensive webbing than *latidisca.* *Ansonia malayana* and *platysoma* also have more extensive webs. *Ansonia hanitschi* differs from *latidisca* in having oval or elongate glandular ridges dorsolaterally.

Range.—Known only from western Borneo.

SARAWAK: First Division, Mount Penrissen. KALIMANTAN: Mount Damus.

Ansonia leptopus (Günther)

Bufo leptopus Günther, 1872, Proc. Zool. Soc. London, **1872**, p. 598—Matang, Sarawak.

Bufo spinulifer Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, 160, pl. 11, fig. 6—Mount Kina Balu, Sabah.

Ansonia leptopus Inger, 1954, Fieldiana, Zool., **33**, p. 239; 1960, *ibid.*, **39**, p. 479, fig. 83A.

Material examined.—Borneo 19 (6 BM, including type of *leptopus*; 2 FMNH; 3 MHNP, type of *spinulifer;* 3 RMNH; 4 SM; 1 ZMB).

Descriptive notes.—A large *Ansonia*, females to 60 mm., males about 35 mm.; finger tips rounded; tip of first finger reaching disk of second; third and fifth toes with at least two phalanges free of web; no tarsal ridge; no interorbital ridges; no light band from eye to arm.

Secondary sex characters.—Six females measure 50.8–60.2 mm. (mean 56.00), even the smallest having mature oviducts. Five males having vocal sacs measure 34.2–35.8 mm. (mean 34.90). The extent of webbing is not subject to sex dimorphism.

The vocal sac is like that in *albomaculata.* Males have two to four rows of black spines under the mandible. A brown nuptial pad covers the dorsal surfaces of the metacarpal and basal phalanx of the first finger. Males usually have four longitudinal rows of large, spinose tubercles on their backs.

Ecological notes.—Two topotypic specimens (FMNH 77449–50) were caught in primary rain forest, presumably the habitat from which the type came. One specimen was perched on a leaf one meter above ground and the second on a rock, both at the edge of a small stream.

The type locality is 140 meters above sea level. The elevations from which the Kina Balu specimens were taken is unknown but should not be less than 900 meters.

Range.—Borneo. Probably widely distributed.

SABAH: Kota Belud District, Mount Kina Balu. SARAWAK: First Division, Lundu, Matang, Santubong; Second Division, Mt. Klingkang; Third Division, Bukit Lila Bulu. KALIMANTAN: Long Hut in the upper Mahakam basin, Liang Kubung.

Ansonia longidigita longidigita Inger

Ansonia longidigita longidigita Inger, 1960, Fieldiana, Zool., **39**, p. 480, figs. 81C, 83B, and 84A—Mount Kina Balu, Sabah.

Bufo leptopus (not of Günther) Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat. (3), **2**, p. 159; Smith, 1931, Bull. Raffles Mus., no. 5, p. 13 (part).

Material examined.—Borneo 72 (9 BM, holotype and paratypes; 31 FMNH, paratypes; 23 MCZ, paratypes; 5 NMB; 4 SM, 3 paratypes).

Descriptive notes.—A large *Ansonia*, females to 65 mm., males to 50; finger tips rounded; tip of first finger reaching disk of second; third and fifth toes with one to two phalanges free of web; no tarsal ridge; a pair of longitudinal ridges or rows of tubercles in interorbital space.

Juveniles have a light stripe along the upper jaw running from below the eye to the arm. They are readily distinguished from juvenile *A. albomaculata* in which the infraorbital light spot is separated from the white band running between eye and arm.

Though similar to *leptopus*, *longidigita* (both subspecies) may be readily distinguished from *leptopus* by the greater extent of webbing (fig. 22I and J).

Secondary sex characters.—Only two females (51.5, 52.4 mm.) contain enlarged ova; one female (63.7 mm.) is larger and seven smaller (46.1–49.1 mm.). The mean snout-vent length of all 10 is 50.11 ± 1.64 mm. The size range (29.0–49.4 mm.) of 28 males having vocal sacs is as wide as that of females; only three males exceed 40 mm. Mean snout-vent length of males is 37.16 ± 0.82 mm.

TABLE 14.—Sex dimorphism in extent of web in *Ansonia longidigita longidigita*.
Free phalanges

	Third toe			Fifth toe		
	1	1½–1⅔	2	1	1½–1⅔	2
	No. specimens			No. specimens		
Males	11	9	4	3	8	13
Females	1	2	7	0	2	8

Males have slightly more extensive webbing than females on both the third and fifth toes (Table 14).

Males have three to six rows of brown or black spines under the mandible. The vocal sac resembles that of *albomaculata*. A yellow or brown nuptial pad occupies the dorsal surfaces of the metacarpal and basal phalanx of the first finger.

Ecological notes.—This toad has been found by day under logs and leaves of rain forest floor far from running water (11 specimens). At

night we have caught it along small forest streams (less than 10 m. wide), usually on gravel bars or banks (18 specimens), but occasionally on low vegetation (2).

Altitudinal range is extensive; specimens for which data are available show the following distribution: 130 m.—24; 180 m.—1; 300 m. —2; 915 m.—9; 1,000 m.—12; 1,280 m.—3; 2,100 m.—1.

Range.—Northern and western Borneo.

SABAH: Kota Belud District, Kenokok, Kiau, and Kadamaian River, Mount Kina Balu; Ranau District, Sungei Liwagu. SARAWAK: Second Division, Lupur River valley; Third Division, Mengiong River; Fourth Division, Long Sinei and Meligong on Akah River; Fifth Division, Lawas, Mount Murud.

Ansonia longidigita gryllivoca Inger

Ansonia longidigita gryllivoca Inger, 1960, Fieldiana, Zool., **39**, p. 483, fig. 84B—Sungei Tawan, Kalabakan, Sabah.

Material examined.—Borneo 34 (25 FMNH, including holotype and paratypes; 9 NSH).

Descriptive notes.—Like *Ansonia l. longidigita* except: interorbital ridges obscure or absent; third and fifth toes rarely (1/23) with more than one phalanx free of web; snout-vent range of adult males 32.8–38.3 mm., mean 35.09 ± 0.96.

Secondary sex characters.—The vocal sac resembles that of male *albomaculata.* Males have one to four rows (usually two or three) of spinose tubercles under the mandible. The dark brown nuptial pad occurs on the first or first and second fingers.

Ecological notes.—Specimens were caught at night while calling from spray-moistened rocks in the bed of a small, forest stream only a few meters above sea level.

Range.—Known only from northeastern Borneo.

SABAH: Lahad Datu District, Sungei Pangaruan; Tawau District, Kalabakan.

Ansonia larva sp.

Material examined.—Borneo 2 lots (FMNH). Limb buds stages VII to X.

This is the same form described and figured in a previous publication (Inger, 1960B, p. 501, fig. 91).

Description.—Body oval, not as depressed as in other larval *Ansonia*; oral disk subequal to width of body; lips expanded; lower lip

with a complete marginal row of short papillae; a row of six or seven thick inframarginal papillae at each corner of oral disk; labial teeth II/III; upper beak divided, halves separated by about one-fourth the length of one half; lower beak single.

Color pale cream above with a dark axial cross.

Total length 11.3–12.2 mm.

Relations.—Adults of *Ansonia albomaculata* and *A. longidigita* have been collected in the upper Baleh basin, from whence these tadpoles come. Unfortunately, none of the tadpoles is sufficiently developed to show any of the diagnostic characters of the adults of any species. They differ from other Bornean *Ansonia* larvae in having the halves of the upper beak narrowly instead of widely separated.

Ecological notes.—Both lots were in quiet water in small clear streams having gravel bottoms. In one case the stream flowed through secondary growth, in the other through primary rain forest.

Localities.—SARAWAK: Third Division, Baleh River near mouth of Putai River, Mengiong River.

Pseudobufo Tschudi

Pseudobufo subasper Tschudi

Pseudobufo subasper Tschudi, 1839, Mem. Soc. Sci. Nat. Neuchâtel, **2**, p. 87—Borneo; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 92, fig. 10; Witte, 1933, Bull. Mus. Roy. Hist. Nat. Belg., **9**, no. 24, p. 7.

Nectes sumatanus Werner, 1900, Zool. Jahrb., Syst., **13**, p. 497, pl. 35, fig. 9—Djapura, Sumatra.

Pseudobufo werneri van Kampen, 1905, Zool. Jahrb., Syst., **22**, p. 711—Indragiri, Sumatra; 1923, *op. cit.*, p. 94.

Material examined.—Borneo 14 (2 AMNH; 2 BM; 1 FMNH; 2 NMB; 5 RMNH; 2 ZMB); Sumatra 4 (1 NHMW, cotype of *sumatranus* Werner; 3 NMB, including cotype of *sumatranus* and holotype of *werneri*); Malaya 3 (SNM).

Taxonomic notes.—The amount of webbing between the fingers, the basis of distinguishing *werneri* from *subasper* (van Kampen, 1905, 1923), is subject to individual variation. The holotype of *werneri* (NMB 1917) has more extensive webbing (two phalanges of fourth finger free of web) than other individuals. Six others seen had 2½ phalanges of the fourth finger free; ten had three phalanges free.

Other characters, such as the tuberculation of the dorsal skin, the length of the hind leg, and the degree to which the thigh projects from the body skin, also show enough individual variation within

samples to account for the differences between the holotype of *werneri* and the specimens of *subasper* with which it was collected.

Description.—A large toad, females to 155 mm.; body stout; limbs heavy; no bony cranial crests; snout obtusely pointed, slightly projecting in profile; nostrils on dorsal surface of head; tympanum distinct, two-thirds to three-fourths eye diameter; no parotoid glands, but entire dorsal and lateral surfaces of head and body covered with round, heterogeneous warts; dorsal, lateral, and ventral skin with fine spinules.

Fingers long, slender, blunt at tips; first finger about half length of second, third longer than snout; fingers webbed at bases; third and fourth fingers with 2–3 phalanges free of web; subarticular tubercles scarcely discernible. Toes with blunt tips, fully webbed to tips; a tarsal ridge; a very weak outer metatarsal tubercle; no subarticular tubercles; fifth toe subequal to third; tibia 0.32–0.34 of snout-vent; length of foot measured from base of inner metatarsal tubercle to tip of fourth toe 0.43–0.48 of snout-vent.

Color (in alcohol) dark brown above and on sides; yellowish below; usually an oblique, orange, dorsolateral stripe.

Secondary sex characters.—Females apparently reach a much larger size than do males. The six females examined that had mature or nearly mature ova measured 91.9–155.0 mm. (mean 121.93); the six males with vocal sacs measured 76.8–93.6 mm. (mean 86.38).

Males have subgular vocal sacs with a single, long opening, which may be on either side of the mouth. The gular skin in mature males is black, that of females yellowish as the rest of the venter. A dark, spinose nuptial pad, of the type characteristic of *Bufo*, covers the dorsal and medial surfaces of the first finger from its base to the beginning or center of the terminal phalanx.

Ecological notes.—All of the recorded specimens of *Pseudobufo* have been caught in lowlands, often in swamps or lakes along the lower reaches of large rivers. In Borneo this type of habitat is best developed in the Kapuas basin of western Borneo and in the complex, anastamosing drainages of southern Borneo.

The dorsally situated nostrils and the long, fully webbed toes are characteristic of aquatic frogs. The only eye-witness account of the behavior of *Pseudobufo* (A. L. Butler, quoted in Boulenger, 1912) stated that males call from vegetation overhanging water into which they dive if disturbed. The same source stated that they were powerful swimmers.

The ova are small (1–1.5 mm.), numerous, and densely pigmented. Presumably the breeding behavior is similar to that of most species of *Bufo*.

Range.—Southern Borneo, eastern Sumatra, and Malaya.

KALIMANTAN: Kuala Kapuas, Muara Teweh, and Telok Betung on Barito River, Sampit, Sanggau, Sintang, Tumbang Hiang.

MICROHYLIDAE

Key to groups of Bornean microhylids.

1A. A small spine-like projection of skin at heel and elbow (fig. 24A); belly yellow with a brown network .... *Chaperina fusca.*

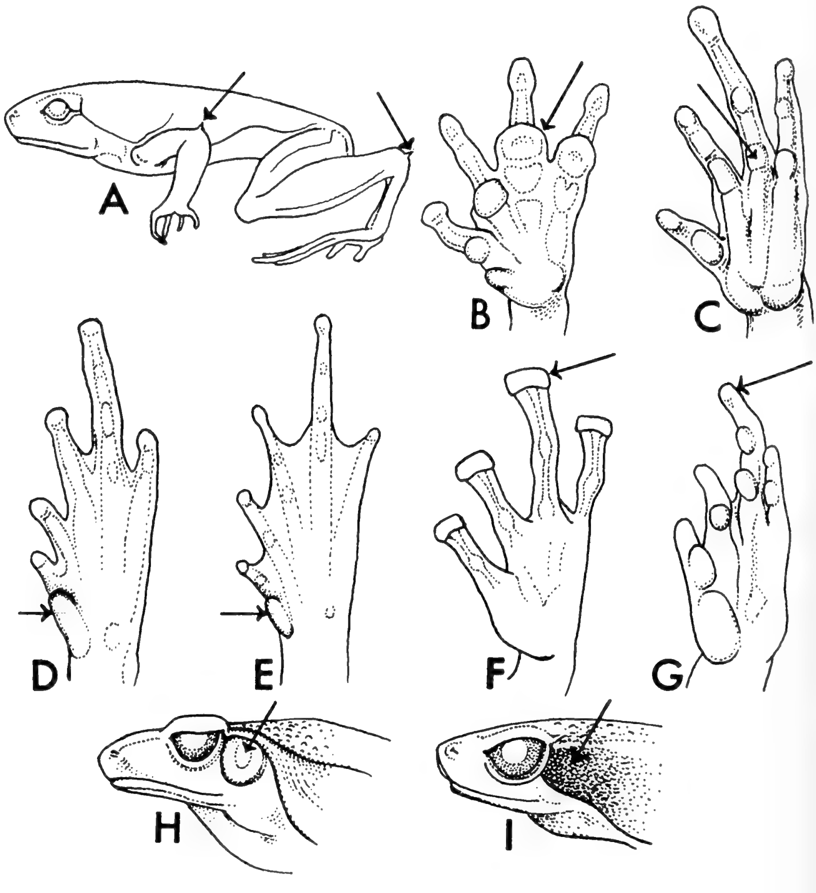


Fig. 24. Key to groups of Microhylidae.

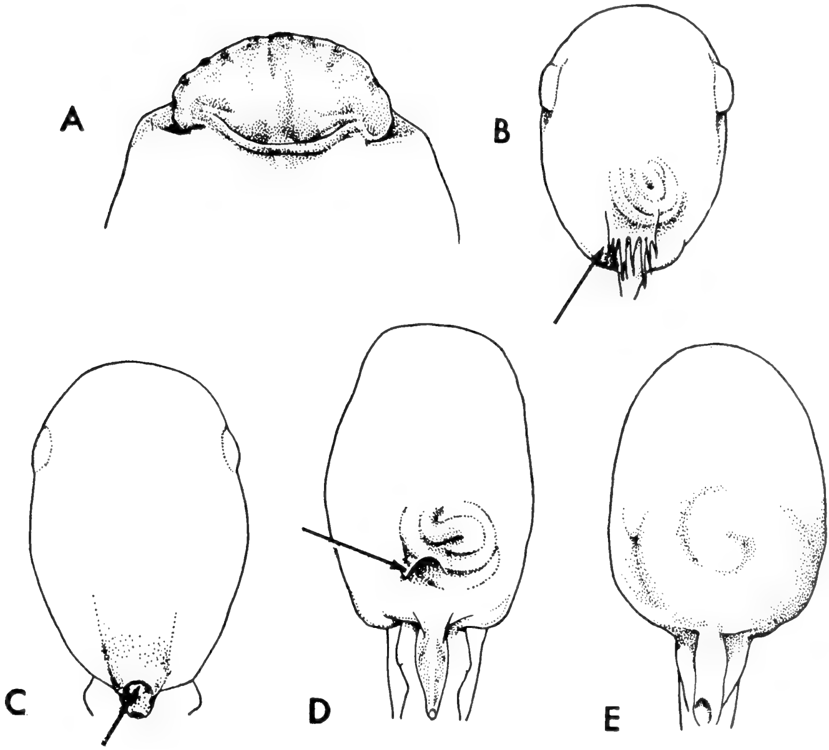


FIG. 25. Key to microhylid tadpoles.

B. No such spines; ventral coloration various . . . . 2.

2A. Underside of fingers with greatly enlarged tubercles (fig. 24B) *Metaphrynella sundana.*

B. Fingers without greatly enlarged tubercles (fig. 24C) . . . . 3.

3A. Snout long, 2—2½ times diameter of eye . . . . *Gastrophrynoides borneensis.*

B. Snout less than twice diameter of eye . . . . 4.

4A. Inner metatarsal tubercle shovel-like, elevated (fig. 24D), more than half length of first toe . . . . 5.

B. Inner metatarsal tubercle low, not shovel-like (fig. 24E) . . . . 6.

5A. Tips of fingers expanded into truncate disks (fig. 24F) . . . . *Kaloula.*

B. Tips of fingers not expanded (fig. 24G) . . . . *Calluella.*

6A. Tympanum visible (fig. 24H) . . . . *Kalophrynus.*

B. Tympanum hidden by skin or absent (fig. 24I) . . . . *Microhyla.*

KEY TO KNOWN LARVAE OF GROUPS OF BORNEAN MICROHYLIDAE

1A. Lower lip expanded (fig. 25A) . . . . *Microhyla* (part).

B. Lower lip not expanded . . . . 2.

2A. Spiracle covered by a flap of skin (fig. 25B), or spiracle with long tube (fig. 25C) . . . . 4.
B. Spiracle without flap or long tube (fig. 25D) . . . . 3.

3A. Gut with numerous coils (fig. 25D) . . . . *Chaperina fusca*.
B. Gut with only one or two coils (fig. 25E) . . . . *Kalophrynus*.

4A. A long spiracular tube opening at end of body (fig. 25C) . . . . *Kaloula*.
B. Spiracle covered by flap that is attached only anteriorly (fig. 25B) . . *Microhyla*.

Calluella Stoliczka

Calluella Stoliczka, 1872, Proc. Asiatic Soc. Bengal, **1872**, p. 146.

Colpoglossus Boulenger, 1904, Ann. Mag. Nat. Hist., (7), **13**, p. 42.

Calliglutus Barbour and Noble, 1916, Proc. New England Zool. Club, **6**, p. 20.

Parker's (1934) diagnoses of *Calluella* and *Colpoglossus* differ in the following ways: clavicle and procoracoid are complete though weak in *Calluella* but reduced to "minute vestiges" in *Colpoglossus*; a small omosternum is present in *Calluella* but not in *Colpoglossus*; the pupil is circular in *Calluella*, vertical in *Colpoglossus*; toes are one-third to two-thirds webbed in *Calluella*, but have only a rudiment of web in *Colpoglossus*.

The difference in webbing between the two species of *Colpoglossus* (*sensu* Parker), which have the toes about one-fourth webbed, and *Calluella guttulata* (toes about one-third webbed) is no greater than the difference between *guttulata* and *Calluella ocellata* Liu (toes fully webbed, according to Liu, 1950).

Both Boulenger (1904) and Parker (1934) stated that the pupil of the holotype of *Colpoglossus brooksi* was vertical. Unfortunately I failed to examine that character in the holotype, but in the two others seen the pupil is round. The pupil of *Colpoglossus smithi* (Barbour and Noble) is round. Thus *Colpoglossus* (*sensu* Parker) does not differ from *Calluella* in pupil shape.

The difference in the pectoral girdles must be considered as a unit because reduction in the procoroids and clavicles is invariably accompanied by reduction or disappearance of the omosternum (see numerous examples in Parker, 1934). Parker describes many instances of reduction in the anterior elements of the pectoral girdle in microhylids and refers (p. 5) to *Calluella* and *Colpoglossus* as examples of reduction beginning at the mesial border. In the former the clavicles are weak mesially and in the latter are reduced to lateral vestiges. Thus the condition in *Colpoglossus* represents a further step in the process begun in *Calluella* and not a different process.

Within other genera of Microhylidae analogous progressive reduction of skeletal elements may be seen. In Malaysian *Microhyla* the degree of reduction of the first finger varies (p. 145). In the genus *Kalophrynus* the degree of reduction of the fourth finger increases from *pleurostigma* to *punctaus* to *bungurantus*.

As previously defined, the genus *Calluella* was distributed from western China (*ocellata* Liu) and southern Burma (*guttulata* Blyth) to Sumatra (*volzi* van Kampen). The generic range of these microhylids is now extended to Borneo.

The two Bornean species, *brooksi* and *smithi*, differ in head shape, in relative length of the hind limb and in coloration. The head is much wider in *brooksi* (head width 1.28–1.43 times its length) than in *smithi* (1.04–1.10). Parker (1934) pointed out that when the leg was pulled forward the tibio-tarsal articulation reached the tympanic region in *brooksi* and the anterior border of the eye in *smithi*. The ratio of tibia to snout-vent length is 0.37–0.39 in three *brooksi* and 0.49–0.51 in three *smithi*. The dorsal pattern in *brooksi* consists of two dark stripes or rows of spots, whereas that of *smithi* is a large central mass with laterally projecting branches. The sides of *smithi* have large, light-edged, black spots; the sides of *brooksi* have very small, dark spots.

Calluella brooksi (Boulenger)

Colpoglossus brooksii Boulenger, 1904, Ann. Mag. Nat. Hist., (7), **13**, p. 43, pl. 2—Bidi, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 97.

Colpoglossus brooksi Parker, 1934, Monogr. Microhylidae, p. 31, figs. 5–6.

Material examined.—Borneo 5 (1 BM, holotype; 1 FMNH; 1 RMNH; 2 SM).

Description.—A medium-sized frog, adults 50–60 mm.; habitus stocky; limbs short; head width 0.43–0.48 of snout-vent, head length 0.31–0.35; head broadly rounded at upper jaw; dorsally snout obtusely pointed or truncate, vertical in profile, longer than diameter of eye; nostril at end of snout; canthus rostralis not distinct; lores sloping, not concave; interorbital three times width of upper eyelid; tympanum present, hidden under skin.

Tips of fingers not expanded; first finger shorter than second; no supernumerary metacarpal tubercles; subarticular tubercles not expanded. Tips of toes not expanded; toes about one-fourth webbed; third and fifth toes with two phalanges free of webbing, fourth toe with four free; toes with narrow fringe of skin to tips; inner metatarsal tubercle compressed, elevated, two-thirds to three-fourths length

of first toe; no outer metatarsal tubercle; tibia 0.37–0.39 of snout-vent.

Skin above and on sides with scattered round tubercles; a weak fold from eye to axilla present or absent; throat coarsely granular, with a row of enlarged tubercles below mandible; chest smooth; abdomen weakly rugose or granular.

Color (in alcohol) brown above; a dark longitudinal stripe beginning on upper eyelid, curving mesad on occiput then laterad and branching over shoulder to form two parallel stripes or rows of spots; pattern broken, forming dark network in some specimens; ventrum yellow, immaculate or with complex brown network on throat and abdomen; limbs dorsally with crossbars and/or a dark network.

Secondary sex characters.—Males are probably smaller than females. Two males having vocal sacs measure 50.8 and 55.2 mm., one female having enlarged ova measures 60.4 mm. The ova are uniformly dark and 2.0–2.5 mm. in diameter.

Males have black throats and median subgular vocal sacs with slit-like openings near the corners of the mouth. Nuptial pads are absent.

Ecological notes.—The enlarged, compressed metatarsal tubercle indicates that *C. brooksi* is a burrower. One male (FMNH 77225) was caught in a shallow rain pool on a road through forest, suggesting the site of oviposition. The dark pigmentation of the ova also indicates an exposed site of oviposition.

All known localities are within 500 meters of sea level.

Range.—Borneo.

SARAWAK: First Division, Bidi, Kuching, Matang. KALIMANTAN: Long Petah.

Calluella smithi (Barbour and Noble)

Calliglutus smithi Barbour and Noble, 1916, Proc. New England Zool. Club, 6, p. 21, pl. 2, text figs. 1–2—Limbang River district, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 98.

Colpoglossus smithi Parker, 1934, Monogr. Microhylidae, p. 32.

Material examined.—Borneo 4 (2 FMNH; 2 MCZ, holotype and paratype).

Description.—A small frog, adult female 39 mm.; habitus stocky, limbs moderate; head slightly wider than long, width 0.36–0.43 of snout-vent, length 0.34–0.39; snout truncate, rounded in profile, longer than diameter of eye; nostril near end of snout; canthus rostralis rounded; lores sloping, not concave; interorbital 2–3 times width of upper eyelid; tympanum present, hidden under skin.

Tips of fingers not expanded; first finger shorter than second; no supernumerary metacarpal tubercles; subarticular tubercles not expanded. Tips of toes swollen into small round disks; toes about one-fourth webbed; third toe with 2½ phalanges free, fifth toe with two, and fourth toe with 3⅔; toes with narrow fringe of skin to tips; inner metatarsal tubercle compressed, elevated, about one-half length of first toe; no outer metatarsal tubercle, tibia 0.49–0.51 of snout-vent.

Skin smooth above and below; a weak fold from eye to axilla.

Color (in alcohol) brown above; back with a large dark marking, wider posteriorly and with laterally projecting branches at shoulder and sacrum or with branches extending between lateral spots; side of head with a black stripe just below canthus, resuming behind eye and expanding in temporal region; sides of body with large, irregular black spots; throat brown, spotted with yellow; abdomen whitish with small brown spots; rear of thigh boldly marked with light-edged dark infra-anal spot and oblique stripes or blotches distally; limbs with dark crossbars dorsally.

In life, the dark markings are edged with pink or red (Barbour and Noble, 1916). The largest specimen has a broad, red arc above the anus.

Ecological notes.—Two females (37–39 mm.), which contained enlarged non-pigmented ova, were found separately under leaves on the floor of primary forest at mid-day at an elevation between 100 and 200 meters. The other two were found in a hole under a rock or log (Barbour and Noble, 1916).

Range.—Borneo.

SARAWAK: Third Division, Mengiong River; Fifth Division, Limbang River district.

Kaloula Gray

The two Bornean species, *baleata* and *pulchra*, are easily distinguished by the extent of the web, which reaches the middle subarticular tubercle on the inner edge of the fourth toe in *baleata* (fig. 24D) but does not extend beyond the basal subarticular tubercle in *pulchra*. Hence *baleata* has three phalanges of the fourth toe free of web and *pulchra* has four.

Kaloula pulchra pulchra Gray

Kaloula pulchra Gray, 1831, Zool. Misc., p. 38—China; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 150.

Kaloula pulchra pulchra Parker, 1934, Monogr. Microhylidae, p. 84, figs. 33–34.

Material examined.—Borneo 1 (FMNH); Celebes 1 (FMNH); Singapore 20 (10 CAS; 10 FMNH); Malaya 6 (1 AMNH; 2 FMNH; 3 SU); Thailand 5 (FMNH); Indo-China 1 (FMNH); Hong Kong 2 (FMNH).

Description.—A moderate-sized frog, adult males to about 70 mm., females to about 75 mm.; habitus stocky, limbs short, knee projecting only slightly from skin of trunk; head much wider than long; snout broadly rounded, vertical or rounded in profile; snout subequal to diameter of eye; nostril midway between eye and tip of snout or closer to tip of snout; canthus rostralis not distinct; lores sloping, weakly concave; interorbital about twice width of upper eyelid; tympanum present, not visible through skin.

Fingers long; tips expanded into truncate disks, that of first finger scarcely wider than penultimate phalanx, that of third finger twice as wide; first finger shorter than second; no supernumerary metacarpal tubercles; subarticular tubercles not expanded. Tips of toes not expanded; web rudimentary, not extending beyond level of proximal subarticular tubercle of fourth toe; third toe longer than fifth; inner metatarsal tubercle compressed, strongly elevated, not as long as first toe; outer metatarsal tubercle transversely oval, not as large as inner tubercle; tibia 0.254–0.348 of snout-vent (median 0.322; $N=16$).

Skin above rugose or tubercular, no folds or ridges; below granular; throat of males coarsely granular.

Color (in alcohol) purplish brown mid-dorsally from groin to between eyes, the dark area much narrowed anteriorly and ending abruptly on line connecting centers of eyelids; a narrow dark, lateral stripe from rear of eye almost to groin; lateral stripe separated from mid-dorsal dark coloration by a light, gray band; usually several yellow or red spots dorsally near groin; head before eyes gray; underside mottled dirty yellowish brown.

Secondary sex characters.—In the only large sample available, that from Singapore, females are slightly larger than males. Six females containing pigmented ova measure 56.6–73.2 mm. (mean 63.55 ± 2.30); 13 males with fully developed secondary sex characters measure 53.8–67.4 mm. (mean 60.88 ± 1.13). The difference between the means is not statistically significant ($P > 0.20$).

The throats of mature males are black and more coarsely granular or rugose than those of females. Males have median subgular vocal sacs with paired, slit-like openings and wide lineae masculinae at dorsal and ventral borders of the obliquus muscle.

Larvae.—The following descriptive notes are taken from Parker (1934).

Body oval, width two-thirds length; body flattened above; snout truncate; eyes lateral; mouth terminal, without beaks or teeth; spiracle median, at end of long tube opening at rear of body; anus median, tube projecting from lower caudal fin.

Tail nearly twice as long as head and body, pointed, crests convex.

Dark brown to black above, lighter and spotted with white below.

Total length 40 mm.; head plus body 14 mm.

Ecological notes.—This species, unknown from natural, undisturbed environments, is locally very abundant in towns and cities in Thailand and in Singapore (Flower, 1899). Butler (1904) saw large breeding aggregations in the town of Kuala Lumpur. This association with man probably has led to its accidental dispersal (Parker, 1934) and to its spotty geographic distribution. One specimen (AMNH 51288) was found on board ship in a cargo of jelutong that had been loaded in "Borneo or Singapore."

Flower (*op. cit.*) said that captive specimens fed on a variety of insects attracted to lights. Large Orthoptera could not be managed because the mouth of *K. pulchra* is too small. Some Hemiptera were not eaten, presumably those such as Pentatomidae that produce a noxious secretion.

Apparently *K. pulchra* breeds after almost every heavy rain fall. Flower (*op. cit.*) heard choruses at night in Singapore during nine months of the year. The large breeding aggregation mentioned by Butler (*op. cit.*) formed at noon following a morning downpour. Any temporary pool may be utilized, some of them so shallow that they dry up in a few days with resultant heavy mortality among the larvae (Butler, *op. cit.*).

Range.—Southern China and Hong Kong to Sumatra and Celebes (Parker, 1934). Parker questioned the occurrence of *pulchra* in Borneo. Van Kampen (1923) included Borneo in the species' range on the basis of a specimen reported from Sarawak by Peters (1872). That specimen (MCG 29468) is a *Microhyla*. The only authentic Bornean record known to me is based on FMNH 75541.

KALIMANTAN: Singkawang.

Kaloula baleata baleata (Müller)

Bombinator baleatus Müller, 1836, Verh. Genootsch. Batavia, **16**, p. 96—Krawang, Java.

Kaloula baleata Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 122; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 148, fig. 21; Parker, 1934, Monogr. Microhylidae, p. 88 (part).

Kaloula baleata baleata Inger, 1954, Fieldiana, Zool., **33**, p. 427.

Material examined.—Borneo 18 (6 BM; 8 FMNH; 1 NMB; 3 RMNH); Celebes 11 (8 BM; 1 FMNH; 1 MCZ; 1 USNM); Java 26 (6 AMNH; 4 MCZ; 16 RMNH); Bali (5 FMNH); Lombok 8 FMNH; Palawan 2 (FMNH).

Description.—A moderate-sized frog, adults to about 66 mm.; habitus stocky, limbs short; head wider than long, broadly rounded at upper jaw; dorsally snout obtusely pointed; snout vertical in profile, equal to or longer than diameter of eye; nostril closer to tip of snout than to eye; canthus rostralis not distinct; lores sloping, not concave; interorbital 1½ to 2 times width of upper eyelid; tympanum present, usually not visible through skin.

Tips of all fingers expanded into truncate disks, those of outer fingers twice as wide as penultimate phalanges; first finger shorter than second; no supernumerary metacarpal tubercles; subarticular tubercles not expanded. Tips of toes not expanded; toes about one-third webbed; first two toes with 1½ phalanges free, third and fifth with two, and fourth with three; web reaching middle subarticular tubercle of fourth toe on inner edge; inner metatarsal tubercle oval, compressed, elevated, about three-fourths as long as first toe (in Bornean populations); outer metatarsal tubercle round, its diameter about half length of inner tubercle, separated from inner tubercle by about its own width; tibia 0.29–0.36 of snout-vent.

Skin above smooth or with low, rounded tubercles; below rugose; throat of male coarsely granular.

Color (in life) dark brown above with a large purplish spot occupying most of mid-dorsum; small orange or red spots at insertions of limbs. In alcohol dark purplish brown above with small, obscure black spots dorsally; red and orange spots fade to pale yellow; below pale or dark brown with small whitish spots.

Secondary sex characters.—As noted elsewhere (Inger, 1954A) *baleata* shows little sex dimorphism. Females from Borneo appear to be slightly larger than males; three mature females measure 54.8–66.5 mm. (mean 61.21) and nine males 49.6–60.6 (mean 55.26). In samples from Palawan and Celebes, females are smaller than males (*ibid.*).

Males have median subgular vocal sacs and blackish, strongly granular gular skin.

Larvae.—Very similar to those of *K. pulchra* (Parker, 1934).

Ecological notes.—Except when breeding, *baleata* is usually fossorial, or semi-fossorial, being found under stones or logs (Taylor, 1922A) or in burrows (Mertens, 1930). Mertens found *baleata* in forests, grasslands, and around houses in the Lesser Sundas. It is apparently abundant in and around towns in Borneo, but seen or heard only after heavy rains. A large chorus formed in a roadside ditch surrounding a grassy field in Sandakan after a rain. Other specimens have been caught in paddy-fields and small ponds around Jesselton. Definite records of *baleata* from forests in Borneo are lacking.

Most Bornean specimens have been collected at low altitudes. The British Museum has one (92.6.3.18) from unknown elevation on Mount Dulit. Parker (1934) records *baleata* from sea level to 1525 meters, the latter based on Javan frogs.

Geographic variation.—The inner metatarsal tubercle is not as large or as elevated in frogs from Borneo as in those from Java and the Lesser Sundas (Table 15). The tubercle is about three-fourths the length of the first toe in Bornean frogs, from three-fourths to slightly

TABLE 15.—Geographic variation of *Kaloula baleata* in size and body proportions.

Locality	No.	Range	Median
		Tibia length[1]	
Borneo	9	285–361	323
Java	6	284–314	305
Bali	5	298–314	309
Lombok	6	297–345	322
	$H^2=5.568$	$P>0.10$	
		Inner metatarsal tubercle[1]	
Borneo	7	50–58	52
Java	21	52–79	62
Bali	5	64–72	66
Lombok	6	64–78	73
	$H^2=20.04$	$P<0.001$	
		Snout-vent (mm.) of males[3]	
Borneo	9	49.6–60.6	55.26 ± 1.36
Palawan	6	43.5–47.0	44.70 ± 0.64
Bali	4	49.8–57.4	52.45
Lombok	5	48.2–56.2	52.42 ± 1.42
Java	10	43.2–53.2	49.13 ± 0.94
	$H^2=18.48$	$P=0.001$	

[1] In terms of thousandths of snout-vent.

[2] H of Kruskal-Wallis test.

[3] All males having vocal sacs and black throats. Mean and standard error are given instead of the median.

longer than the toe in Javan frogs, and usually longer than the toe in frogs from the Lesser Sundas.

Geographic variation in the relative length of the tibia is not statistically significant (Table 15).

Bornean males are larger than those from other islands; Palawan males are apparently the smallest (Table 15).

The differences between this subspecies and *baleata kalingensis* have been discussed elsewhere (Inger, 1954A).

Range.—Malay Peninsula to Flores in the Lesser Sundas (Parker, 1934), Celebes, Borneo, and Palawan.

SABAH: Jesselton District, Inanam, Jesselton; Sandakan District, Sandakan. SARAWAK: Third Division, Mount Dulit; Fourth Division, Akah River. KALIMANTAN: Tumbang Bunut on the Rungan River, "southeastern Borneo," Pontianak (van Kampen, 1923).

Kalophrynus Tschudi

Three species differing in size, relative development of the fingers, coloration, and secondary sex characters, were found at each of two collecting sites in the Fourth Division, Sarawak. The largest (males 47–49 mm.) of the three has light-rimmed, black inguinal ocelli; the part of the fourth finger projecting from the palm is longer than the terminal phalanx of the third finger; there are two tubercles under the fourth finger; males have a nuptial pad on the fingers and distinct spines on the back. This form is clearly *K. pleurostigma.*

The two others are about half the size of *pleurostigma.* One, which has a light stripe on the snout and side and light spots in a large inguinal area or a single dark-edged light inguinal ocellus, is so similar to the original description and illustration of *K. heterochirus* (Boulenger, 1900) as to leave little doubt about the identification. The adult female type of *heterochirus* measured 27 mm.; adult females in the present series measure 30.5–32.9 mm. Males are 24–27 mm. The part of the fourth finger projecting from the palm in these frogs is shorter than the last joint of the third finger; there are two tubercles under the fourth finger; males have neither a nuptial pad nor spines on the back, but do have an extensive gland on the inner anterior aspect of the upper arm.

The third form is smaller still. Males having vocal sacs measure 21–24 mm., and females with enlarged ova 26–27 mm. Six of 11 individuals have a round light spot on the anterior surface of the thigh; two have an ill-defined black inguinal area; none has the in-

guinal coloration of *heterochirus* or *pleurostigma* (see above). About half have a faint light lateral stripe. The part of the fourth finger projecting from the palm is shorter than the terminal phalanx of the third finger; there is only one tubercle under the fourth finger distal to the palmar tubercle instead of two, as in *heterochirus* and *pleurostigma*. Males lack nuptial pads, spines on the back and axillary region, and humeral glands. The absence of these secondary sex characters does not result from immaturity or seasonal fluctuation, as these males were caught while calling. None of the names in the literature seem to apply to this form, which I am designating as a new species, *subterrestris* (see below, p. 137).

At a second locality in Sarawak (Third Division), two groups of specimens were collected. One is the ubiquitous *K. pleurostigma,* and like all Bornean specimens of this species, these have the side of the body distinctly darker than the back and light-rimmed inguinal ocelli. The other species is much smaller (adult females 38–41 mm.) lacks inguinal ocelli, has the side lighter than the back, and has a short fourth finger as in the two small species mentioned above. It therefore differs from *pleurostigma* in size, coloration, and relative development of the fingers. Unfortunately no males were caught so that the secondary sex characters are unknown. This form is also unreported in the literature; I am applying the name *intermedius* to it (see below, p. 131).

Although *intermedius* agrees with *heterochirus* and *subterrestris* in having the third toe longer than the fifth and a short fourth finger, it is larger than both (Table 16) and differs from *heterochirus* in lacking a light lateral stripe and light inguinal spots, and from *subterrestris* in having two instead of one tubercle under the fourth finger. *K. intermedius* is probably larger than the fifth Bornean species, *punctatus*, considering the small amount of sexual dimorphism shown by this genus (Table 16); it also differs from *punctatus* in having the third toe projecting farther than the fifth.

Kalophrynus subterrestris differs from *punctatus* in the characters just mentioned and in having only one tubercle beneath the fourth finger instead of two. The two *punctatus* I have seen are reddish brown above and the eleven *subterrestris* black or dark gray. Differences between *subterrestris* and *heterochirus* and between the former and *pleurostigma* are given in preceding paragraphs and in Table 16.

Kalophrynus heterochirus differs from *punctatus* in the relative lengths of the third and fifth toes and in the presence of the gland on the upper arm of males. *K. heterochirus* was placed in the synonymy

TABLE 16.—Comparison of species of *Kalophrynus* Tschudi.

	Species of *Kalophrynus*						
	pleuro-stigma	*robin-soni*[1]	*punc-tatus*	*bungu-ranus*	*hetero-chirus*	*subter-restris*	*inter-medius*
Male sex characters:[2]							
nuptial pad with many minute spines	+	0	0	0	0	0	—
nuptial pad with few large spines	0	+	0	0	0	0	—
spines on back	+	0	0	+	0	0	—
spines on upper arm	0	0	0	+	0	0	—
gland on upper arm	0	0	0	0	+	0	—
Size (mm.) of adults:							
females							
no.	8	—	—	2	6	4	2
range	35.2–57.8	—	—	25.5–26.7	30.5–32.9	25.8–27.0	37.9–40.5
mean	46.16[3]	18	—	26.1	31.4	26.5	39.2
males							
no.	13	—	1	3	10	6	—
range	37.0–50.4	—	—	22.2–23.4	24.1–27.2	21.0–23.4	—
mean	43.83[3]	17	22.8	22.9	26.3	22.6	—
Extent of third and fifth toes	3>5	3>5	3<5	3>5	3>5	3>5	3>5
Tubercles under fourth finger	2	—	2	2	2	1	2

[1] Data from Parker (1934). [2] + indicates presence; 0 indicates absence. No males of *intermedius* are known.
[3] Size data on *pleurostigma* based solely on Bornean specimens.

of *K. bunguranus* Boulenger (type locality Natuna Islands) by Parker (1934). Topotypic males of *bunguranus* differ from those of *heterochirus* in several secondary sex characters (Table 16). Furthermore, both sexes of *bunguranus*[1] have black inguinal spots in a light area instead of light spots in a dark area as in *heterochirus*. The separation of these two forms at the specific level should be maintained.

Kalophrynus punctatus is much smaller than *pleurostigma*, has a relatively longer fifth toe and a shorter fourth finger than the latter, and also differs in the male secondary sex characters (Table 16). This is the only species in which the fourth finger projects as far as the first.

The one species apparently confined to the mainland is *K. robinsoni*, the smallest species in the genus. According to Parker (1934), males of *robinsoni* have rows of large, conical spines on the first three fingers.

A key to the species of this genus follows.

1. Fifth toe projecting as far as or farther than third toe (fig. 26A) . . . . . *punctatus*.
   Fifth toe not projecting as far as third (fig. 26B) . . . . . 2.
2. Portion of fourth finger projecting from palm shorter than terminal phalanx of third finger (fig. 26C) . . . . . 3.
   Portion of fourth finger projecting from palm longer than terminal phalanx of third finger (fig. 26D) . . . . . *pleurostigma*.
3. Only one tubercle under fourth finger between palmar tubercle and tip of finger *subterrestris*.
   Two tubercles under fourth finger . . . . . 4.
4. A light stripe or line along canthus, extending back along side almost to groin . 5.
   No light stripe or line on snout or side . . . . . 6.
5. A dark inguinal ocellus surrounded by a light area . . . . . *bunguranus*.
   Light inguinal spots in a large dark area . . . . . *heterochirus*.
6. Adult females about 18 mm. . . . . . *robinsoni*.
   Adult females 38-40 mm. . . . . . *intermedius*.

Kalophrynus heterochirus Boulenger

Calophrynus heterochirus Boulenger, 1900, Proc. Zool. Soc. London, **1900**, p. 186, pl. 17, fig. 4—Limbang, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 104.

Kalophrynus bunguranus (part) Parker, 1928, Ann. Mag. Nat. Hist., (10), **2**, p. 473; 1934, Monogr. Microhylidae, p. 100.

Material examined.—Borneo 21 (20 FMNH; 1 RMNH).

Taxonomic notes.—Reasons for recognizing *heterochirus* as distinct from *bunguranus* (Günther) are given above.

[1] Four syntypes (BM 1947.2.11.38–41) and one topotype (NHMW 3994) of *bunguranus* were examined in this study.

Description.—A small microhylid, males ca. 26 mm., females ca. 30 mm.; habitus slender (males) to stocky (females); snout obtusely pointed or truncate, equal to or shorter than diameter of eye; nostril

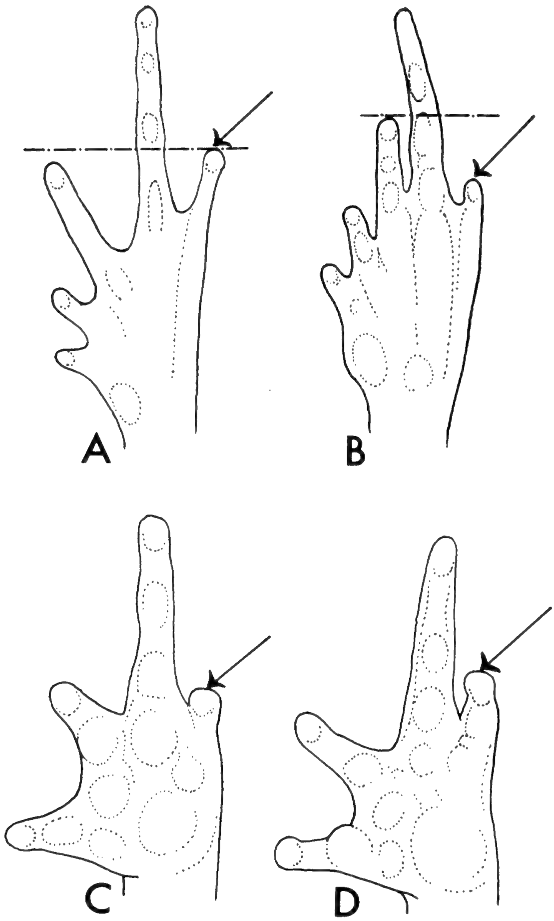


FIG. 26. Key to species of *Kalophrynus.*

closer to tip of snout than to eye; interorbital $1\frac{2}{3}$–2 times width of upper eyelid; tympanum distinct, about one-half diameter of eye.

Tips of fingers and toes rounded; first finger slightly shorter than second; third finger longest, equal to diameter of eye; fourth finger shortest, portion projecting from palm shorter than terminal phalanx of third finger; two tubercles between palmar tubercle and tip of

fourth finger. Third toe projecting farther than fifth; web to distal edge of distal subarticular tubercle of third toe; subarticular tubercles conspicuous on all but fifth toe; tibia 0.39–0.42 of snout-vent.

Skin coarsely granular; a thick gland on side of head behind tympanum, gland with a sinuous anterior border.

Color (in life) purplish brown above; a narrow light stripe along canthus, continued above tympanum, and running obliquely to lower part of groin; light stripe bordered below by thin dark line; one or more bluish white spots in a black inguinal area; similar light spots behind thigh in a few specimens. In alcohol side of head and body below stripes usually much lighter than back; ventral surfaces whitish, immaculate or with varying amounts of dark pigment on throat and chest.

Secondary sex characters.—See p. 126 and Table 16. Both females contain enlarged ova. Males have slit-like vocal sac openings.

Ecological notes.—Eighteen of the frogs examined were collected in hilly primary forest; another specimen was caught in a small clearing in forest. Eighteen were on the floor, seven of them under fallen leaves. A pair was found in amplexus in a hole in a fallen tree. Six of the males were calling when caught between 11 and 23 hours.

Range.—Borneo.

SARAWAK: Fourth Division, Nyabau, Labang, Sungei Pesu; Fifth Division, Limbang (Parker, 1934). KALIMANTAN: Long Bluu.

Kalophrynus intermedius new species

Holotype.—Field Museum of Natural History 139348, an adult female collected at Nanga Tekalit, Mengiong River, Third Division, Sarawak, by F. Wayne King on March 15, 1963.

Diagnosis.—An intermediate-sized species of *Kalophrynus*, adult females 35–40 mm.; clavicle and procoracoid well-developed; third toe longer than fifth; projection of fourth finger from palm shorter than terminal phalanx of third finger; two tubercles under fourth finger; no light lateral stripe; no inguinal ocelli.

Description.—Habitus stocky, limbs short; snout obtuse, projecting, slightly longer than diameter of eye; nostril closer to tip of snout than to eye; canthus distinct, lores vertical; interorbital $1\frac{1}{2}$–$1\frac{2}{3}$ width of upper eyelid; tympanum distinct, about $\frac{2}{3}$ diameter of eye; a crenulated ridge of skin on palate at front of pharynx, preceded by a shorter, more strongly notched one.

Tips of fingers and toes rounded; first finger shorter than second; third finger much the longest, longer than diameter of eye; only tip of fourth finger projecting from palm, free portion of finger shorter than terminal phalanx of third finger; two tubercles between the palmar tubercle and the tip of the fourth finger. Third toe projecting farther than fifth; only tips of first, second, and fifth toes projecting beyond web; third toe webbed to distal edge of distal subarticular tubercle of third toe; subarticular tubercles of first four toes strongly elevated, that of fifth toe scarcely discernible; two low metatarsal tubercles; tibia 0.38–0.41 of snout-vent.

Skin everywhere granular; skin of back with thick glandular layer; a thick gland on side of head behind tympanum, delimited by a sinuous groove from eye above and behind tympanum to axilla, and curving over insertion of arm.

Color (in alcohol) brown or purplish brown above; holotype with obscure dark marking, others unmarked; sides yellow or cream-colored; dorsal and lateral coloration meet at a sharp boundary with a dark line at boundary in two of three specimens; no inguinal spots; ventrally cream-colored, with pink tinge on throat, throat with two irregular, dark, longitudinal bands; a few small, dark spots on anterior portion of abdomen; rear of thighs dark brown, without spots.

Measurements (mm.) of holotype: snout-vent 40.5; head width 13.1; tibia 15.5.

Paratypes.—FMNH 138070, 144298, from type locality. The first is an adult female (37.9 mm.) containing enlarged, pigmented ova. The second is an immature female (32.4 mm.) in which the oviduct is slender and straight.

Ecological notes.—All three frogs were collected on the floor of primary rain forest between 100 and 300 meters above sea level.

Comparisons.—See p. 127.

Range.—Known only from the type locality.

Kalophrynus pleurostigma pleurostigma Tschudi. Fig. 27.

Kalophrynus pleurostigma Tschudi, 1838, Mem. Soc. Sci. Neuchâtel, **2**, p. 86—Sumatra; Smith, 1925, Sarawak Mus. Jour., **3**, p. 31; 1931, Bull. Raffles Mus., no. 5, p. 21.

Kalophrynus pleurostigma pleurostigma Parker, 1934, Monogr. Microhylidae, p. 97; Inger, 1956, Fieldiana, Zool., **34**, p. 396.

Calophrynus pleurostigma van Kampen, 1923, Amph. Indo-Austr. Arch., p. 102, fig. 12.

Material examined.—Borneo 46+5 larval series (1 AMNH; 6 BM; 24+5 larval series FMNH; 1 MCZ; 2 NHMW; 3 RMNH; 7 SM; 2 ZMA); Sumatra 6 (1 RMNH; 1 USNM; 4 ZMA); Malaya 4 (1 FMNH; 3 SU).

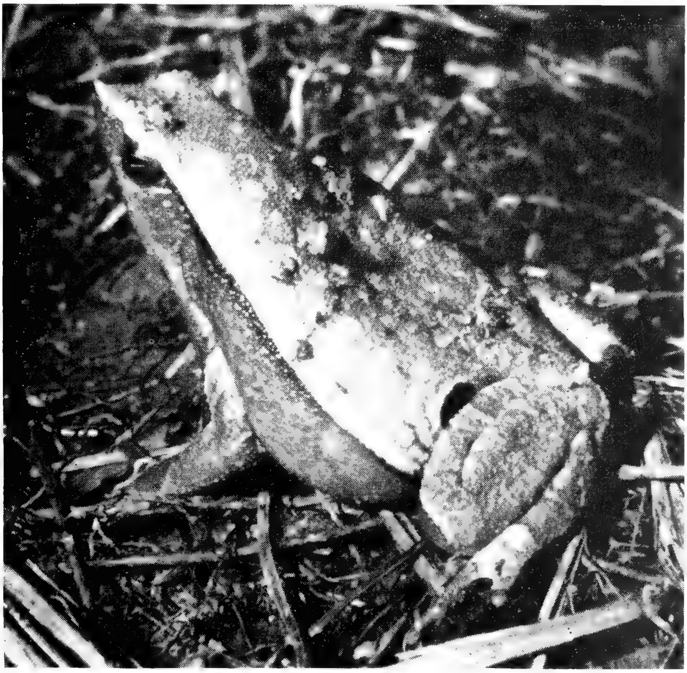


FIG. 27. *Kalophrynus pleurostigma*, 49 mm.

Taxonomic notes.—The subspecies of *K. pleurostigma* appear to be founded on weak grounds. The only difference between the nominate form and *p. interlineatus* mentioned by Parker (1934, p. 99) that may be valid is the extent of webbing. Geographic variation in that character is complicated by sex dimorphism. The four specimens (MCZ 4869–70; USNM 103450, 103452) I have seen from the range of *p. interlineatus* have slightly less webbing than do Bornean and Sumatran frogs. As a sample of four is too small for judging a variable character, I am simply following Parker's arrangement.

Description.—A medium-sized microhylid, adult males to about 50 mm., females to 58 (Table 16); habitus stout, body widest at sacrum; head wider than long; snout pointed, projecting, equal to diameter of eye; nostril closer to tip of snout than to eye; interorbital about 1⅔

times width of upper eyelid; tympanum usually distinct, ½–¾ diameter of eye.

Finger tips rounded, not expanded; first and fourth shorter than second; fourth finger one-third to two-fifths length of third; third finger longer than diameter of eye; projection of fourth finger from palm and web greater than width of finger; subarticular tubercles prominent. Tips of toes like those of fingers; third toe longer than fifth; first, second, third, and fifth each with one phalanx free of web, fourth toe with 3–3⅓ phalanges free; an oval inner metatarsal tubercle; a round outer metatarsal tubercle present or absent; tibia 0.36–0.46 of snout-vent (median 0.392; N=15).

TABLE 17.—Comparison of sex dimorphism in *Kalophrynus pleurostigma* from Borneo and Mindanao.[1]

	Extent of web on fifth toe[2]		
	Distal edge of tubercle	Between tubercle and swollen tip	Base of swollen tip
Mindanao ♂	—	4	24
" ♀	6	2	—
Borneo ♂	—	4	7
" ♀	—	3	5

[1] Data from Inger, 1954A.
[2] Table gives number of individuals.

Skin granular above and below, coarsely granular on abdomen; a curved supratympanic fold from eye to axilla.

Color (in alcohol) dark reddish brown above; sides of head and body usually darker than back, the two shades meeting at a sharp oblique dark line; a black ocellus at each groin; pattern of back highly variable; usually dark crossbars on dorsal surface of hind limb; below yellowish white, often with brown suffusion on throat and sometimes with small dark spots on abdomen.

The commonest dorsal pattern in the Bornean sample consists of a dark area between the shoulders having a short spur to each eye and a long, oblique stripe to each groin. In some frogs the dark pigment forms a complex network; in others it is restricted to a few black spots. A few specimens have no dorsal markings other than the inguinal ocelli.

Secondary sex characters.—The Bornean sample shows less sex dimorphism in size or extent of webbing than does the Philippine population (Tables 16 and 17).

Bornean males do, however, have nuptial pads on the first three fingers, white dorsal asperities, and median subgular vocal sacs as described for Philippine males (Inger, 1954A).

Larvae and development.—Reasons for assigning these larval series (FMNH 63522–26) to *K. pleurostigma* are given elsewhere (Inger, 1956).

Body subspherical, flattened above, snout truncate; eyes lateral, visible from below; spiracle median, about midway between eye and end of body; vent median, at end of long tube; tail 1⅓–2 times head-plus-body, lanceolate, tip bluntly rounded, margins of fins subparallel; fins deeper than caudal muscle beyond proximal third.

Mouth terminal; no beaks; lips not expanded; no labial teeth or papillae.

Larvae without hind limb buds gray, lighter ventrally. Metamorphosing larvae dark blackish brown above and on sides; belly gray; green-gold flecks on head and back.

Total length of mature larva 9 mm.

At temperatures between 24° and 29° C., only 16 days are required for development from early gastrulation to resorption of tail. The gut of the tadpole has only two loops visible ventrally and appears to be full of yolk. The larvae do not feed but complete development on the energy supplied by the yolk.

Ecological notes.—All 18 frogs for which data are available were collected at ground level, mostly under leaves, in primary forest. The larval series mentioned above was found in very shallow water in a log in primary rain forest. Five males were caught in other small temporary bodies of water, three at the bases of trees and two in road ruts. *Kalophrynus pleurostigma* has been found breeding in rain-filled road ruts in the Philippine Islands (Inger, 1954A).

Eight of the Bornean adults were caught within 100 meters of sea level, as were the five larval series. Six adults were taken between 100 and 200 meters, one at 1200, two at 1675 (Smith, 1931A), and one at 2195 meters. Nine others are from unknown elevations. In Mindanao the altitudinal range of *pleurostigma* is from sea level to over 1000 meters (Inger, 1954A).

Geographic variation.—As noted above (*Secondary sex characters*), sex dimorphism in size and webbing is more pronounced in the Mindanao sample than in that from Borneo.

The fourth finger is slightly longer in Mindanao frogs, being equal to or very slightly shorter than the eye-nostril distance, whereas in

frogs from Borneo (12 measured), Sumatra (5), Malaya (3), and Thailand (2) the finger is $\frac{1}{2}$ to $\frac{2}{3}$ the eye-nostril distance.

Range.—The southern part of the Malay Peninsula (Parker, 1934), Sumatra, Leyte, Mindanao, Basilan, Siragao, and Borneo. The subspecies *K. p. interlineatus* occurs on Java (Mertens, 1957).

SABAH: Kinabatangan District, Bukit Kretam; Kota Belud District, Kamborangah, Lumu Lumu (Smith, 1931A); Labuk District, Beluran, Paitan; Tawau District, Brantian River Estate. SARAWAK: First Division, Bidi (Parker, 1934), Kuching; Third Division, Mount Dulit, Mengiong River; Fourth Division, Akah River, Baram River, Niah; Fifth Division, Trusan River, Pa Brayong. KALIMANTAN: Batangalai (van Kampen, 1923), Mount Damus, Kenepai Mountains, Long Bluu, Pagat, Sebruang River (*ibid.*), Semberrah River.

Kalophrynus punctatus Peters

Calophrynus punctatus Peters, 1871, Monatsber. Akad. Wiss. Berlin, **1871**, p. 579—Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 104.

Kalophrynus punctatus Parker, 1934, Monogr. Microhylidae, p. 101.

Material examined.—Borneo 2 (1 MCG, holotype of *punctatus*; 1 RMNH).

Description.—A small microhylid, mature males 22–27 mm.; habitus stout, body widest in sacral region; head broader than long; snout obtusely pointed, projecting, equal to eye or slightly shorter; nostril closer to tip of snout than to eye; interorbital about $1\frac{1}{3}$ times width of upper eyelid; tympanum obscured by skin but visible, one-half diameter of eye.

Finger tips rounded, not expanded; first and second fingers subequal, fourth slightly shorter than second and slightly shorter than half length of third; third finger equal to or slightly shorter than diameter of eye; projection of fourth finger from palm and web exceeds width of finger; subarticular tubercles prominent. Tips of toes like those of fingers; fifth equal to or longer than third; toes with thick webbing at their bases; third and fifth toes with two phalanges free of webbing, fourth toe with four free; a large, rounded inner metatarsal tubercle; no outer metatarsal tubercle; tibia 0.39 of snout-vent length.

Skin granular above and below.

Color (in alcohol) reddish brown above; sides of head and body darker brown; back with or without small black spots; ventrally dusky with round, light spots (Parker, 1934) or pale yellowish white with a dark band under jaw and smaller dark spots posteriorly.

Secondary sex characters.—The Semedum specimen (RMNH, unnumbered) and the holotype (MCG 29130) are males having long, slit-like vocal sac openings on each side of their tongues. I did not find nuptial pads or other asperities that might be interpreted as secondary sex characters. The holotype measures 27 mm. (Parker, 1934), the second specimen 22.8 mm.

Range.—Mentawei Islands (Boulenger, 1894B) and Borneo. Presumably it will be found in Sumatra eventually.

SARAWAK. KALIMANTAN: Mount Semedum.

Kalophrynus subterrestris[1] new species figure. 28.

Holotype.—Field Museum of Natural History 150421, an adult male collected at Sungei Seran, Labang, Bintulu District, Fourth Division, Sarawak, by James P. Bacon, Jr. and William Hosmer on December 13, 1963.

FIG. 28. *Kalophrynus subterrestris*, paratype (FMNH 150424), 27 mm.

[1] This specific name is chosen because of the discovery of two specimens in a burrow.

Diagnosis.—A small species of *Kalophrynus*, males about 23 mm., females about 27 mm.; third toe projecting farther than fifth; only one tubercle between palmar tubercle and tip of fourth finger.

Description.—Habitus moderately stocky, limbs short; snout obtusely pointed, projecting, subequal to diameter of eye; nostril closer to tip of snout than to eye; canthus rostralis distinct, lores vertical; interorbital $1\frac{1}{3}$–$1\frac{3}{5}$ width of upper eyelid; tympanum distinct $\frac{1}{2}$–$\frac{2}{3}$ diameter of eye; a crenulated palatal ridge at front of pharynx, preceded by an angular, more strongly notched one.

Tips of fingers and toes rounded; first finger shorter than second; third finger longest, equal to diameter of eye; portion of fourth finger projecting from palm much shorter than last phalanx of third finger; only one tubercle between palmar tubercle and tip of fourth finger. Third toe projecting farther than fifth; web to base or center of distal subarticular tubercle of third toe; conspicuous subarticular tubercles on first four toes only; two low metatarsal tubercles; tibia 0.40–0.45 of snout-vent (median 0.423).

Skin coarsely granular; no gland or fold behind tympanum on side of head.

Color (in life) dark gray above; no light stripe on snout; usually no light line on side; sides of body lighter than back; inguinal region with or without a dark spot; side of body near groin orange. In alcohol, black or dark gray above; throat and chest with varying extent and density of black mottling; belly whitish, with or without dark spots; rear of thigh without sharp lines or sharply defined bands of color; no ocelli on rear of thigh.

Measurements (mm.) of holotype: snout-vent 23.4; tibia 9.9; foot 8.4; head width 7.4.

Paratypes.—FMNH 150422–26, two females and three males, all adult, from the type locality; FMNH 157652–56, two males, one female, and two juveniles from Sungei Pesu, Tubau, Bintulu District, Fourth Division, Sarawak; FMNH 140238, an adult female from the lower Segama River, Sabah.

Variation in the paratypes is dealt with in *Description* and below.

Secondary sex characters.—Three females contain enlarged ova measuring 1.8–2.0 mm. The females are about 4 mm. larger than the males (Table 16).

Males have slit-like vocal sac openings but lack the glands and asperities found in other species (Table 16).

Ecological notes.—Ten of the 12 specimens were collected on the floor of primary forest on hillsides. Five were found under leaves or other debris on the forest floor and two in a burrow. Four of the males, caught on separate occasions between 14 and 21 hours, were calling. The sound of one led to the discovery of the burrow, which was 600 mm. deep and topped by a mound of clay 43 mm. high and 170 mm. at its maximum width. It is not at all certain that the frog actually excavated the burrow.

Comparisons.—See pp. 126–129.

Range.—Known only from Borneo. Detailed localities given above.

Kalophrynus sp.

Microhyla borneensis Parker, 1934, Monogr. Microhylidae, p. 128 (part).

Parker (1934) assigned a developmental series of tadpoles (BM 1914.5.12.61–78) from Kuching to *Microhyla borneensis*. Parker mentioned a yolk-filled gut and noted little change in size in the developmental series. Pre-limb bud larvae in this series measure 6.0 mm. (6.5 according to Parker). One in Stage XI has a total length of 9.5 mm. and a body length of 3.6 mm. Snout-vent length in a Stage XX tadpole is 4.0 mm. The small size, lack of significant growth, and feebly-coiled yolk-filled gut suggest that the entire larval period is supported by yolk and that no food is ingested.

These are the only putative *Microhyla* larvae that may have such a modified existence. A similar mode of larval life is known in *Kalophrynus pleurostigma* (p. 135). The identification of the larvae of *K. pleurostigma* was based on the form of the pectoral girdle in a metamorphosed young from a developmental series (Inger, 1956).

The larvae assigned to *M. borneensis* by Parker differ from the *K. pleurostigma* series only in having pointed tails rather than rounded ones. General body and tail form are similar; the position and form of spiracular openings are identical. Larvae of *K. pleurostigma* in limb bud stages are 8–9 mm., total length, and a Stage XX tadpole has a snout-vent length of 4 mm. (*ibid.*); these sizes are virtually identical to those cited above for the Kuching series. The overall agreement of these two sets of larvae leaves little doubt that the latter are also *Kalophrynus*.

The discovery of the Kuching series in the pitcher of a *Nephenthes* (Parker, 1934) suggests that the adults were smaller than the average *K. pleurostigma*. The difference in tail shape also indicates that the Kuching larvae are a second species of *Kalophrynus*.

Description.—Head and body flattened above, spheroidal below, much deeper in pre-limb bud larvae than in older ones; snout rounded; eyes lateral, visible from below; mouth terminal, with feebly expanded lower lip; spiracle median, opening three-fourths of distance from tip of snout to end of body; no free flap over spiracle; anal tube directed obliquely backward, opening at edge of ventral fin.

Caudal muscle weak, tapering gradually; dorsal fin with a straight margin, not as deep as caudal muscle, about one-half to three-fifths depth of ventral fin; latter convex, about equal to depth of caudal muscle at end of first quarter of tail; tail tapering gradually to a very short terminal filament.

Color (in alcohol) pale yellow, with fine dark dots on dorsal and lateral surfaces of body and on caudal muscle; fins colorless.

Range.—Borneo.

SARAWAK: First Division, Kuching.

Chaperina Mocquard

Chaperina fusca Mocquard

Chaperina fusca Mocquard, 1892, Le Naturaliste, (2), **6**, p. 35—Sintang, Borneo; Smith, 1931, Bull. Raffles Mus., no. 5, p. 21; Parker, 1934, Monogr. Microhylidae, p. 103, figs. 41–42; Inger, 1954, Fieldiana, Zool., **33**, p. 414; 1956, *ibid.*, **34**, p. 398.

Sphenophryne fusca van Kampen, 1923, Amph. Indo-Austr. Arch., p. 109; Smith, 1930, *loc. cit.*, no. 3, p. 124, fig. 12.

Microhyla leucostigma Boulenger, 1899, Ann. Mag. Nat. Hist., (7), **3**, p. 275, pl. 12, fig 1—Larut, Perak; van Kampen, 1923, *op. cit.*, p. 156; Witte, 1933, Bull. Mus. Hist. Nat. Belg., **9**, no. 24, p. 7.

Sphenophryne leucostigma Smith, 1925, Sarawak Mus. Jour., **3**, p. 12; *ibid.*, p. 31.

Nectophryne picturata Smith, 1921, Jour. Fed. Malay States Mus., **10**, p. 198, pl. 2, fig. 2—Mount Dulit, Sarawak.

Material examined.—Borneo 76+tadpoles (2 AMNH; 2 BM; 37+11 series of tadpoles FMNH; 24 MCZ; 3 RMNH; 8 SM); Malaya 1 (BM); Palawan 2 (1 FMNH; 1 MCZ).

Description.—A small frog, adult males to 21 mm., females to 26 mm.; habitus slender to moderately stocky; limbs long; head as wide as long or longer than wide; snout rounded, projecting, rounded in profile, longer than eye; nostril slightly closer to tip of snout than to eye; canthus not distinct; lores almost vertical, not concave; interorbital 1½–2 times width of upper eyelid; tympanum present, usually not visible through skin.

Tips of three outer fingers distinctly expanded into round disks almost twice width of penultimate phalanges; tip of first finger not or very little expanded; first finger about half length of second; subarticular tubercles small, round. Tips of toes with disks similar in size and shape to that of third finger; first four toes not webbed beyond basal subarticular tubercles; first and second toes with two phalanges free, third with three, fourth with four, and fifth with $2\frac{1}{3}$–$2\frac{1}{2}$ free; inner metatarsal tubercle low, oval; no outer metatarsal tubercle; tibia 0.49–0.56 of snout-vent.

Elbow and heel each with a fine conical, dermal projection (ca. 0.5–1.0 mm.); skin above smooth or with low warts; a fold from eye to axilla; sides with low, round warts; ventral surfaces smooth.

Color (in life) black above with many green flecks on head and back; white dots on sides; below large yellow spots separated by a dark brown network. In alcohol, dorsum blackish brown with or without large black spots; green spots absent; small white spots on sides; ventral spots fade to cream; in some individuals the throat lacks yellow spots or has only a few small spots.

Secondary sex characters.—Males are slightly but significantly smaller than females. Thirty-two adult males from Borneo measure 17.8–20.7 mm., snout to vent (mean 19.17 ± 0.12); 13 mature females from Borneo measure 19.6–24.4 mm. (mean 22.44 ± 0.33). Males have longer legs than do females. The ratio of tibia to snout-vent is 0.495–0.562 (median 0.535) in 27 males and 0.489–0.523 (median 0.507) in 13 females.

Males have median subgular vocal sacs with slit-like openings on each side of the mouth. Nuptial pads and other secondary sex characters are lacking, even though males were caught in breeding aggregations.

Larvae.—The identification of larvae described earlier (Inger, 1956) was based upon a series some of which were reared to metamorphosis.

Body oblong; eyes superolateral; mouth terminal, without expanded lips, labial teeth, horny beaks, or papillae; spiracle median ventral, tube attached dorsally, opening three-fourths of distance from tip of snout to end of body; anus opening at end of long tube attached to ventral fin, dextral; tail not as deep as body, tapering gradually to a point; dorsal fin equals depth of caudal muscle beyond center of tail.

Color in life black above, light below; eye black, usually with conspicuous light triangle in upper part of iris; caudal muscle with dark dorsal line, gray below; ventral fin colorless; dorsal fin gray adjacent to muscle.

Tadpole in Stage XII 23 mm. total length, body 8 mm. Two in Stage XXI 24–26 mm. total length, body 9 mm.

Ecological notes.—All except one of the 34 frogs for which I have detailed information were caught in primary rain forest. The exceptional specimen was in the cut stem of a bamboo in old secondary growth. *Chaperina* lives on the ground as well as in low vegetation. Four groups of calling males were found, each in small rain-filled holes never more than 15 cm. deep and always in water black with humus. Two of the holes were on the upper surface of horizontal logs and two in the forest floor. These choruses were active only by day.

Larvae were later collected from one of the holes in the ground and from one of those in a log. Other small, rain-filled depressions in the immediate vicinity lacked putrid material and did not contain larvae or adults. The humus-rich water may support a particular set of infusorians on which *Chaperina* larvae feed.

Chaperina fusca is relatively common within 100 meters of sea level but ranges up to 1800 meters in Borneo (Smith, 1925A); 51 of those seen were caught within 100 meters of sea level, four at 500 meters, and two at 900–1000 meters. On Palawan and in Malaya *fusca* has been caught as high as 1200 meters.

Breeding aggregations were observed in April and June. The breeding period is almost certainly more extensive than that.

Geographic variation.—Frogs from the vicinity of Kuching (AMNH 6728–9; MCZ 3823–5, 3868–71, 3873, 3878–9) have distinct dark spots on their brown backs. All other preserved specimens have uniform dark brown backs.

Range.—Perak, Borneo, and the southern Philippine Islands (Inger, 1954A). The species probably occurs in Sumatra, though it has not been recorded from there yet.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot, Pintasan; Kota Belud District, Kiau (Smith, 1931A), Kenokok; Tawau District, Kalabakan. SARAWAK: First Division, Kuching; Third Division, headwaters of Baleh River, Mount Dulit (Smith, 1921B); Fourth Division, Baram (Parker, 1934), Patah River; Fifth Division, Mount Murud. KALIMANTAN: Betung (de Witte, 1933), Nunukan Island, Sintang.

Metaphrynella Parker

Metaphrynella sundana (Peters)

Calohyla sundana Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**, p. 35—Pontianak, Borneo.

Metaphrynella sundana Parker, 1934, Monogr. Microhylidae, p. 108; Inger, 1956, Fieldiana, Zool., **34**, p. 399.

Material examined.—Borneo 16 (15 FMNH; 1 USNM).

Description.—A small frog, adults up to about 25 mm.; habitus stocky, limbs moderately short; head as wide as long; snout truncate or obtusely pointed, usually projecting, oblique in profile, slightly longer than diameter of eye; canthus rostralis rounded; lores vertical, not concave; interorbital 1⅔–2 times width of upper eyelid; tympanum visible, though somewhat obscured by skin, about $^{3}/_{5}$ diameter of eye.

Tips dilated into truncate disks, not as wide as tympanum; first finger shorter than second; prepollex not enlarged; subarticular tubercles greatly enlarged; fingers webbed to beyond basal tubercles. Tips of toes truncate but not expanded; subarticular tubercles slightly enlarged, much smaller than those of fingers; fourth toe with only two tubercles; web extensive, first three toes and fifth each with one phalanx free of web, fourth toe with 2½ phalanges free; a weak, oval, inner metatarsal tubercle; no outer metatarsal tubercle; tibia 0.42–0.46.

Skin above and below with rounded tubercles; sides with larger tubercles; a curved supratympanic fold from eye to axilla.

Color (in alcohol) gray or brown above, with irregular dark markings; throat gray with black spots or black, not sexually dimorphic; chest and abdomen usually mottled with brown or black; dorsal surfaces of limbs with or without dark crossbars.

Secondary sex characters.—The only female seen contains enlarged ova (ca. 1 mm.) and measures 23.4 mm. The males (all with vocal sacs) range from 19.0 to 22.5 mm. (mean 20.87 ± 0.28 mm.; $N = 15$).

The males have median subgular vocal sacs with slit-like openings on each side of the mouth. Nuptial pads are absent.

Ecological notes.—*Metaphrynella sundana* is found in tree holes in primary or logged rain forest (Inger, 1956), especially in flat, low-lying areas. Males call at night from holes that are usually between 1 and 5 meters above the ground.

With one exception, all known specimens have been collected within 200 meters of sea level. The exception is a specimen (FMNH 128130) caught at 760 meters.

The gravid female (FMNH 63504) was collected in May and a set of eggs, tentatively assigned to this species (Inger, 1956), in June. Males were calling in every month from April to August.

Range.—Borneo.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Sandakan District, Sapagaya Forest Reserve. SARAWAK: First Division, Kuching (Parker, 1934); Fourth Division, Niah, Peluan. KALIMANTAN: Pontianak (*ibid.*).

Gastrophrynoides Noble

Gastrophrynoides borneensis (Boulenger)

Engystoma borneense Boulenger, 1897, Ann. Mag. Nat. Hist., (6), **19**, p. 108—Baram District, Sarawak.

Gastrophrynoides borneensis Noble, 1926, Amer. Mus. Nat. Hist. Novit., no. 212, p. 22, figs. 8–9.

Gastrophrynoides borneense Parker, 1934, Monogr. Microhylidae, p. 104, fig. 43.

Gastrophryne borneensis van Kampen, 1923, Amph. Indo-Austr. Arch., p. 124; Smith, 1925, Sarawak Mus. Jour., **3**, p. 32.

Material examined.—Borneo 7 (2 BM, including holotype; 4 FMNH; 1 SM); ?Sumatra 1 (NMB).

Description.—A small frog, adult females to 41 mm.; habitus stocky, limbs moderately short; head wider than long; snout conical, projecting, rounded in profile, 2–2½ times diameter of eye; nostril closer to tip of snout than to eye; canthus rostralis not distinct; lores sloping, not concave; interorbital 2–2½ times width of upper eyelid; tympanum present, usually obscured by skin, two-thirds to three-fourths diameter of eye.

Tips of outer fingers expanded into small, round disks; first finger shorter than second; second and third fingers with a ridge of skin on inner edges; subarticular tubercles weak. Toes with swollen tips larger than those of fingers; webbing not extending beyond basal subarticular tubercles; an oval inner, but no outer, metatarsal tubercle; tibia 0.43–0.48 of snout-vent.

Skin smooth; a weak fold from eye to axilla.

Color (in alcohol) brown above, yellow below; dorsal surfaces with scattered, small, light spots.

Three females measure 29.8–37.6 mm. (mean 32.4). The largest and smallest contain enlarged, non-pigmented ova.

Ecological notes.—Six specimens were collected within 200 meters of sea level. The holotype, from an uncertain part of the Baram basin, was almost certainly caught below 1000 meters.

Three specimens were found under leaves on the floor of primary rain forest.

Range.—Borneo and, possibly, Sumatra.

The only specimen recorded from Sumatra (NMB 2281) was collected by A. Buxtorf. The Basel catalogue reads, "Probably S. Sumatra: Palembang (prob. East Borneo)." Buxtorf's collection also included two specimens (NMB 2272–3) of *Phrynella pulchra* with the catalogue notations "S. O. Borneo, probably Bandjermasin;" these are the only specimens of *P. pulchra* reported from Borneo. The locality labels of the two series may have been switched. The Sumatran record of *G. borneensis* and the Bornean record of *P. pulchra* need confirmation before they are accepted.

SARAWAK: First Division, Kuching; Third Division, Mengiong River; Fourth Division, Baram District.

Microhyla Tschudi

This genus has a tendency towards shortening of the first finger analogous to reduction of the outer finger in *Kalophrynus*. The first finger projects out of the palm relatively far in *Microhyla berdmorei* (fig. 24C), *Microhyla butleri* (fig. 29A), and *Microhyla heymonsi*, much

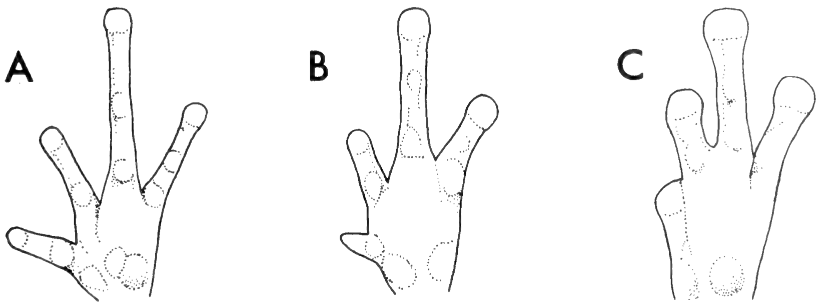


FIG. 29. Hands of *Microhyla butleri* (A), *M. borneensis* (B), and *M. annectens* (C).

less in *Microhyla borneensis* (fig. 29B), and the least in Bornean *Microhyla annectens* (fig. 29C).

The first three species have two phalanges in the first finger, the last two species only one. The relative lengths of the parts of the first finger of these species are given in Table 18.

Adults of the three species of *Microhyla* known from Borneo may be distinguished by means of the following key.

TABLE 18.—Relative lengths[1] of segments of first finger in various species of *Microhyla*.

Species	Mus. No.[2]	Snout-Vent (mm.)	Metacarpal	Phalanges Basal	Phalanges Distal
butleri	100992	19.8	40	30	15
heymonsi	100987	17.3	35	15	8
berdmorei	RMNH	25.2	60	30	20
borneensis	77223	17.4	30	15	0
annectens	77224	15.4	40	5	0

[1] Lengths given in terms of ocular micrometer units under 50 × magnification.
[2] Numbers are those of Field Museum of Natural History except where otherwise noted.

1A. One metatarsal tubercle; first finger not (or barely) projecting from palm ... *annectens.*
B. Two metatarsal tubercles; first finger various ... 2.
2A. Third and fifth toes webbed to disks ... *berdmorei.*
B. Third and fifth toes not webbed to disks ... *borneensis.*

Three species of larvae are known from Borneo. One is clearly the young of *annectens* (p. 148), a second is assigned to *borneensis* (p. 152), and the third cannot be assigned to known adults. The larvae of *berdmorei* from the mainland described by Parker (1934) differ from all three types of Bornean larvae. The three species of larvae and that assigned by Parker to *berdmorei* may be distinguished with the aid of the key below.

1A. Lower lip expanded to form a "funnel mouth" *Microhyla* sp. (FMNH 83032).
B. Lower lip not forming a funnel mouth ... 2.
2A. Anal tube sloping obliquely backward to edge of ventral fin ... *annectens.*
B. Anal tube vertical or recurved along posterior edge of body ... 3.
3A. Tail with a long terminal filament ... *borneensis.*
B. Tail without terminal filament ... *berdmorei.*

Microhyla annectens Boulenger

Microhyla annectens Boulenger, 1900, Ann. Mag. Nat. Hist., (7), **6**, p. 188—Larut Hills, Malaya; Parker, 1934, Monogr. Microhylidae, p. 129.

Material examined.—Malaya 3 (BM, including 2 cotypes): Borneo 10+larvae (FMNH).

Taxonomic notes.—The Bornean sample, which includes both sexes, is tentatively assigned to this species. All frogs have the third and fifth toes fully webbed to the disks in contrast to an adult Malayan male (BM 1928.11.12.1; 19.7 mm.) in which one phalanx of the

fifth toe and two of the third are free of web. The Bornean frogs also lack the black labial spot found in Malayan *annectens*. The first finger does not project from the palm at all in the Bornean frogs and consists of a metacarpal and one very short phalanx. In the Malayan specimens the first finger is about one-third the length of the third; a phalangeal count was not made.

These differences suggest specific divergence. However, with so few specimens available from Malaya, I prefer to postpone recognition of the Bornean population as a named taxon.

The following description is based on the Bornean frogs.

Description.—A small frog, male about 15 mm., females to 19 mm.; body moderately stout; limbs long; head as wide as long; snout obtusely pointed, projecting, oblique in profile; snout longer than eye; nostril equidistant between eye and tip of snout or nearer to latter; canthus rostralis obtuse; lores vertical, not concave; interorbital twice width of upper eyelid; tympanum absent.

Tips of three outer fingers dilated into round disks having weak indications of median, longitudinal groove dorsally; first finger not projecting from palm, only one phalanx, finger lacking subarticular tubercle; three outer fingers with distinct web basally; outer palmar tubercle not divided. Tips of toes with disks wider than that of third finger; dorsal surface of disks with median groove; broad web reaching disks of all toes except fourth, which has two phalanges free; an oval inner, but no outer metatarsal tubercle; tibia 0.68–0.75 of snout-vent.

Skin smooth above and below except on throat (see *Secondary sex characters*); a fold from eye to axilla.

Color (in alcohol) clay brown or gray above; an obscure, wide, dark area beginning between shoulders and covering dorsum; anterolateral corners of dark area with black spots; an oblique, light brown, dorsolateral band; an oblique dark area below dorsolateral light band, the dark area having a black spot or a narrow, interrupted black line along its upper margin; upper lip without dark spot; a narrow light streak from eye to axilla followed by a broad gray or dark brown temporal spot; dorsal surfaces of hind limbs with dark cross bars; a wide or narrow infra-anal black spot; venter white with faint dark mottling.

Secondary sex characters.—The male has a median subgular vocal sac with a slit-like opening on each side of the mouth. The gular skin is wrinkled and bounded posteriorly by a shallow fold, which is continuous laterally with the temporal fold. The male's chin is black.

Two females containing enlarged eggs measure 17.4 and 18.7 mm. Four males having vocal sacs measure 14.9–15.4 mm. (mean 15.2).

Larvae.—Five series of tadpoles from two Bornean localities and covering all ages from pre-limb bud to early metamorphic stages are almost certainly the larvae of this species. An adult (FMNH 77224) was caught in the small pool from which three of the lots were collected. Older larvae (Stages XVIII–XX) have fully webbed toes, distinct disks on the toes, a single metatarsal tubercle, and an extremely shortened first finger.

Of the four Malaysian species of *Microhyla* having extremely reduced first fingers, *borneensis* and *superciliaris* have two metatarsal tubercles. A third species, *annamensis*, known only from Annam, differs from these larvae in having tuberculate skin. The fourth species is *annectens*.

The following combination of characters distinguishes these larvae from all other of *Microhyla* so far reported from Malaysia:

Lips not expanded into funnel; tail with a caudal filament; anal tube running diagonally backwards to edge of ventral fin, no posteriorly directed branch.

The following description is based on the entire developmental series.

Head and body oval, flattened above, spheroidal ventrally, width about two-thirds length; snout broadly rounded; eyes lateral, visible from below; distance between nostrils (open only in Stage XVIII and beyond) one-fourth to one-third interorbital distance; mouth terminal, lips not expanded; lower lip with a median longitudinal notch, covered by upper lip; spiracle median, opening $^4/_5$ to $^9/_{10}$ of distance from tip of snout to end of body; spiracle covered by a free flap of skin frilled on its posterior border, flap usually reaching end of body

TABLE 19.—Length (mm.) and tail ratio in larvae of *Microhyla annectens* from Sarawak.

Stage	Total length	Head plus body	Tail/total
Pre-limb bud	7.9	3.1	0.61
III	11.4	4.5	0.60
XI	14.8–14.9 (2)	5.6–6.2	0.58–0.62
XIII	15.2	5.4	0.64
XV	15.3–15.6 (2)	6.1–6.2	0.60
XVI	17.7	6.5	0.63
XVII	18.8	6.7	0.64
XVIII	14.4 (1)	5.8–6.6 (3)	0.60 (1)
XIX	13.8	5.8	0.58
XX	—	5.9	—

or beyond; anal tube running obliquely backward to edge of ventral fin, without posteriorly directed branch.

Caudal muscle weak; tail tapered abruptly, with a long terminal filament; dorsal fin beginning at end of body, rising beyond proximal fourth, one-half to three-fifths depth of ventral fin; both fins deeper than caudal muscle beyond proximal third.

Color (in life) jet black above, whitish below; caudal muscle black; fins colorless except for a broad, vertical black band crossing both fins in third quarter of tail.

Length and body proportions are given in Table 19.

Ecological notes.—Four males were collected in and around small water-filled holes in rocky banks of small rain forest streams. Three other adults were caught on the floor of primary rain forest.

All sets of larvae were found in holes of the type just mentioned. Most of these holes, which are very common in the rocky streams in the hills of central Sarawak, are between 20 and 150 cm. long and about 15 to 30 cm. deep. These holes are generally 30 to 150 cm. above the "normal" level of the streams but are flooded after every hard rain. Tadpoles of this species were the most conspicuous larvae in or beside rain forest streams of this part of Borneo.

The Bornean specimens were collected between 20 and 200 meters above sea level.

Geographic variation.—Assuming that the Bornean frogs have been correctly assigned, *Microhyla annectens* varies geographically in extent of webbing, coloration, and length of the first finger (for details see *Taxonomic notes*).

Range.—Malay Peninsula and Borneo.

SABAH: Kinabatangan District, Tegupi River. SARAWAK: Third Division, Baleh River near mouth of Putai River, Mengiong River.

Microhyla berdmorei (Blyth)

Engystoma berdmorei Blyth, 1856, Jour. Asiatic Soc. Bengal, **24**, p. 720—Pegu, Burma.

Microhyla berdmorii Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 166; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 158.

Microhyla berdmorei Parker, 1934, Monogr. Microhylidae, p. 127.

Material examined.—Borneo 4 (1 NMB; 3 RMNH); Sumatra 2 (NMB); Thailand 2 (FMNH); Annam 5 larvae (BM).

Description.—A small frog, adult males about 25 mm., females about 30 mm., habitus moderately stout; limbs long; head about as

broad as long; snout obtusely pointed, rounded in profile, projecting slightly; snout longer than eye; nostril closer to tip of snout than to eye; canthus rostralis rounded, lores sloping, weakly concave; interorbital wider than upper eyelid; tympanum present, not visible through skin.

Tips of fingers slightly wider than basal phalanges, dorsal surfaces of disks with a median, longitudinal groove; first finger one-third length of third, subarticular tubercle of first finger distinct, distad from palm; subarticular tubercles not expanded; fingers with fringes of skin. Tips of toes twice as wide as those of fingers; dorsal surfaces of disks with longitudinal grooves; broad web reaching disks of all toes; an oval inner and a smaller, round outer metatarsal tubercle; tibia 0.63–0.70 of snout-vent.

Skin with very small, scattered tubercles on back, larger ones on sides above arms; an obscure tympanic fold from eye to axilla; gular region smooth in females, rugose in males; posterior abdominal skin rugose.

Color (in alcohol) brown above, with an obscure dark marking between shoulders; no crossbars on legs, ventromedian edge of lower leg with several large dark brown spots; rear of thigh with a blackish longitudinal band reaching anus; ventrum whitish, throat of males mottled with dark brown.

Secondary sex characters.—Three females containing enlarged ova measure 26.9–31.9 mm., snout to vent (mean 29.0), and three males having vocal sacs 24.8–28.0 mm. (mean 26.0).

The males have slit-like openings to the median, subgular vocal sac. The males lack nuptial asperities.

Larva.—Parker's description (1934) of the Annamese tadpoles he assigned to *Microhyla berdmorei* should be amplified with the following notes based on the same series.

Lips not expanded; spiracle opening about $^6/_7$ of distance from tip of snout to end of body; spiracle covered by a short bilobed flap wider than long; anal tube running vertically to edge of ventral fin, without posterior branch; ventral fin deeper than dorsal but less than twice as deep; both fins deeper than caudal muscle beyond proximal fourth; nostrils open in Stage XVII tadpole.

Total length of Stage XIV larva 23.1 mm., head-body length 9.6; total length of Stage XVII larva 21.0, head-body 9.1.

Geographic variation.—The outer palmar tubercle is divided by a shallow groove in the two Thailand frogs (FMNH 124239–40) but not in those from Borneo and Sumatra.

Range.—Burma and northern Thailand (Parker, 1934) to Sumatra and Borneo.

KALIMANTAN: Bandjermasin, Long Bluu.

Microhyla borneensis Parker

Microhyla borneense Parker, 1926, Ann. Mag. Nat. Hist. (10), **2**, p. 473—Bidi, Sarawak.

Microhyla borneensis Parker, 1934, Monogr. Microhylidae, p. 128.

Microhyla annectens (part) Boulenger, 1912, Fauna Malay Penin., Rept. and Batr., p. 262; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 156; Smith, 1925, Sarawak Mus. Jour., **3**, p. 32.

Material examined.—Borneo 12+larvae (2 BM, including holotype; 9+larvae FMNH; 1 MCG).

Description.—A small frog, adult males about 18 mm., females about 23 mm.; body moderately stout; limbs long; head broader than long; snout obtusely pointed, rounded in profile, projecting, snout longer than eye; nostril closer to tip of snout than to eye; canthus rostralis rounded; lores sloping, weakly concave; interorbital twice width of upper eyelid; tympanum absent.

Tips of three outer fingers slightly wider than basal phalanges, dorsal surfaces of disks with median longitudinal groove; first finger less than one-third length of third (0.16–0.29); fingers without fringes; subarticular tubercle of first finger distinct, at most half its length lies distad from palm; subarticular tubercles not expanded; outer palmar tubercles not divided. Tips of toes twice as wide as those of fingers; dorsal surfaces of disks with longitudinal grooves; broad web not reaching disks of first and second toes, third toe with two phalanges free, fourth toe with 3–3⅓ free, and fifth toe with 1½–2 free; an oval inner metatarsal tubercle and a smaller, round outer one; tibia 0.62–0.70 of snout-vent.

Skin above smooth or with scattered, low tubercles; a curved temporal fold from eye to axilla; sides with tubercles or low ridges; ventrally smooth except for a few wrinkles at rear of abdomen.

Color (in alcohol) reddish brown or clay brown above; an obscure dark pattern with expansions between the eyes, at the shoulders, and sacrally; lips spotted with black; a broken, narrow, black lateral stripe beginning above arm and extending half length of trunk; a dark round spot surrounding anus; hind limb with or without dark crossbars dorsally; median edge of tarsus with dark spots; throat mottled with brown; rest of venter whitish, with or without small dark spots.

Secondary sex characters.—The two females containing enlarged ova measure 22.8–23.0 mm., three adult males 17.6–18.4 mm. The males have slit-like openings to the vocal sac. Nuptial asperities are absent.

Larvae.—Parker (1934) assigned a series of larvae from Kuching to this species. Reasons are given above (p. 139) for identifying the Kuching larvae as *Kalophrynus.*

Two large developmental series of tadpoles in Stage VI to XX from the Third and Fourth Divisions, Sarawak are probably the young of *M. borneensis.* The oldest stage is sufficiently advanced to recognize the adult form of the pectoral girdle and the limbs. The absence of clavicle, procoracoid, omosternum, enlarged subarticular tubercles, and dermal spines and heel at elbow eliminate *Kaloula, Kalophrynus, Chaperina, Gastrophrynoides, Metaphrynella, Phrynella,* and *Calluella* as possible parents.

The characters that, taken in combination, distinguish these larvae from those of other Malaysian *Microhyla* are: absence of "funnel mouth;" tail tapering to a long drawn out filament, dorsal fin very low in proximal third of tail, at most one-fourth depth of ventral fin; spiracle covered by a long flap that reaches end of body; anal tube curving downward and forward, paralleling rear of body, and opening at edge of ventral fin.

The tadpoles lacking funnel mouths and described by Parker (1934) differ from this series in at least one of the above characters. The tadpoles of *Microhyla berdmorei* (BM 1928.11.15.27–31) have no filament at the end of the tail, have very short flaps over the spiracle, and have much deeper dorsal fins (more than half depth of ventral fin). The larvae of *Microhyla palmipes* have a short spiracular flap and lack a caudal filament (Parker, 1934). The larva of *M. butleri* (BM 1928.11.15.17–20) has a deeper dorsal fin (about half depth of ventral) and a long anal tube directed vertically to the edge of the ventral fin then running posteriorly along the edge of the fin. Larvae of *okinavensis, ornata,* and *pulchra* have deeper dorsal fins (about half depth of ventral) and shorter spiracular flaps.

Metamorphosing individuals have slightly expanded toe disks that have longitudinal dorsal grooves and an outer metatarsal tubercle One or two phalanges of each toe are free of webbing. The first finger is distinct, but short and is about one-fifth to one-fourth the length of the third finger. These characteristics agree only with *borneensis* among the three species of adults of *Microhyla* now known from Borneo.

The following description is based on the entire series.

Head and body flattened above, spheroidal below; width of head one-half to two-thirds head-body length; snout broadly rounded, almost truncate; eyes lateral, visible from below; distance between narial eminences (or nostrils in older larvae) about one-fourth to one-third interorbital distance; mouth terminal, no expanded lips; lower lip with a median, longitudinal notch, covered by upper lip; spiracle opening median, one-fifth to one-fourth the distance from the end of the body to the tip of the snout; a long, wide flap of skin, free on its lateral margins, covering spiracle and reaching to end of body; anal tube vertical, slightly recurved to follow end of body, opening at edge of ventral fin without posteriorly directed branch.

Caudal muscle strong, myomeres beginning high on body, distance of imaginary line connecting eyes from first caudal myomere equal to diameter of eye; tail tapering gradually, drawn out into a long filament; dorsal fin very low in proximal third of tail, less than one-fourth depth of ventral fin, margin straight; ventral fin deeper than caudal muscle at all points.

Color (in alcohol) gray above, a uniform dusting of melanophores on dorsal and lateral surfaces of head and body; head and body without pigment below except in Stage XX larva; caudal muscle and dorsal fin densely pigmented; ventral fin very faintly pigmented proximally, becoming progressively darker towards tip.

Head-body lengths in Stages VII–IX (4 specimens) were 7.6–9.8 mm., total lengths 26.1–31.0 mm., ratio of tail to total 0.68–0.71. In Stages XVII–XVIII (2 larvae) head-body lengths were 10.0 mm., total lengths 31.3–32.0 mm., ratio of tail to total 0.68–0.69.

Ecological notes.—One specimen was caught hopping on the floor and four others found under leaves on the floor of primary rain forest. Ten of the known adults and both series of larvae were found less than 300 meters above sea level. The altitude from which both the Mount Dulit and Matang specimens came were not recorded (Smith, 1925B).

Tadpoles were obtained from a small isolated pool near the crest of a forested hill.

Range.—Borneo.

SABAH: Kinabatangan District, Tegupi River; Sandakan District, Sandakan, Sepilok. SARAWAK: First Division, Bidi, Kuching, Matang (Smith, 1925B); Third Division, Mount Dulit, Mengiong River; Fourth Division, Long Akah.

Microhyla sp.

Several lots of microhylid larvae (FMNH 83032, 137971–3) from Sarawak differ from larvae described by Parker (1934). The lower lip in these is expanded forming a "funnel mouth" typical of certain species of *Microhyla.* The two Malaysian species known to have this modification, *heymonsi* and *achatina,* have not been reported from Borneo. The former occurs in Southeast Asia and Sumatra and the latter in Java (Parker, 1934). The tadpoles of both have a long anal tube directed vertically and opening where it meets the edge of the ventral fin. The Sarawak tadpoles have a vertically directed anal tube that turns sharply posteriorly near the edge of the fin for a distance about equal to the diameter of the eye.

The tadpoles of *Microphyla achatina* and *heymonsi* have knob-like structures on each side of the mouth. In *heymonsi* the knob is flat; in *achatina* it has a central depression. The Sarawak tadpole has a knob like that of *achatina.*

The dorsal fin of the Sarawak larvae is pigmentless in the anterior two-thirds, and densely pigmented from there to the terminal filament, which is pigmentless. The ventral fin is colorless in the anterior half and densely pigmented from there to the terminal filament. The tadpole of *achatina* (BM.1928.11.17.1–3) has the dorsal fin densely pigmented except in the terminal filament, and the ventral fin pigmented only in the middle third. The caudal pattern of larval *heymonsi* (FMNH 100999, 101001, 109490) is identical to that of *achatina.*

The first finger of the Stage XVIII tadpole is about one-fourth the length of the third finger. The toes of this tadpole have distinct disks and are fully webbed.

Description.—Head and body oval, flattened above, spheroidal below; width of head about two-thirds head-body length; snout broadly rounded; eyes lateral, visible from below, diameter about one-ninth head-body length; distance between narial eminences one-fourth inter-orbital distance; mouth terminal-superior, lower lip expanded, a knob-like structure with a central depression on each side of mouth; spiracle opening median, two-thirds of distance from tip of snout to end of body; a short flap (about one-ninth head-body length) free on its lateral margins covering spiracular opening, flap not reaching end of body; anal tube vertical with a posteriorly-directed arm along edge of ventral fin.

Caudal muscle moderate; tail tapering abruptly near tip and ending in a short filament; dorsal fin less than half depth of ventral; ventral fin deeper than caudal muscle beyond proximal fourth.

Head, body, and caudal muscle gray; dorsal fin pigmentless in anterior two-thirds; black in last third except for colorless terminal filament; ventral fin colorless in anterior third or half and in terminal filament, black in remainder.

Stage XV larva total length 13.8 mm., head-body length 4.9; Stage XVIII larva total length 19.7 mm., head-body length 6.6.

Ecological notes.—Three of these series were obtained in small (ca. 0.5×1.0 m.), isolated pools of water near the tops of forested hills, which were between 250 and 350 meters above sea level. Two of these pools also contained larvae of *Rhacophorus fasciatus*.

SARAWAK: Third Division, Mengiong River; Fourth Division, Long Akah.

RANIDAE

KEY TO GENERA OF BORNEAN RANIDAE.

1A. Mandible with a single median cusp . . . . *Ooeidozyga.*
B. Mandible with a median and two lateral cusps, or with lateral cusps only . . 2.

2A. Two outer metatarsals separated by a groove or by webbing . . . . 3.
B. Two outer metatarsals not separated from each other . . . . *Micrixalus.*

3A. Tips of toes expanded into disks having circummarginal, horizontal grooves 4.
B. Tips of toes expanded or not, but always lacking horizontal, circummarginal grooves . . . . *Rana* (part).

4A. Disks of fingers and toes having a distinct transverse groove proximally on ventral surface . . . . *Staurois.*
B. Disks without transverse, proximal groove . . . . 5.

5A. Anterior-most part of choana near its lateral rim; males with humeral glands *Rana* (part).
B. Anterior-most part of choana near its median rim; males without humeral glands . . . . *Amolops.*

KEY TO TADPOLES OF GENERA OF BORNEAN RANIDAE.

1A. A large abdominal sucker (fig. 51) . . . . *Amolops.*
B. No abdominal sucker . . . . 2.

2A. No rows of labial teeth . . . . *Ooeidozyga.*
B. Lips with rows of teeth . . . . 3.

3A. Lower lip with 4 to 6 rows of papillae (fig. 49) . . . . *Staurois.*
B. Lower lip with 1 or 2 rows of papillae . . . . *Rana.*

KEY TO BORNEAN SPECIES OF *Rana*

1A. A light dorsolateral stripe or line on each side, beginning at tip of snout (fig. 30A) . . . . 2.
B. Usually without dorsolateral light stripe; if present stripe begins behind eye . . . . 3.

2A. Numerous light spots middorsally . . . . *signata.*
B. No light spots middorsally . . . . *luctuosa.*

3A. Tips of outer fingers about twice width of basal phalanges (fig. 30B) . . . . . 4.
B. Tips of outer fingers less than twice width of basal phalanges (fig. 30C, D) . . 5.

4A. No outer metatarsal tubercle on foot (fig. 30E) . . . . *hosei.*
B. Outer metatarsal tubercle present (fig. 30F) . . . . *chalconota.*

5A. Tympanum not visible through skin (fig. 30G) . . . . 6.
B. Tympanum clearly visible (fig. 30H) . . . . 7.

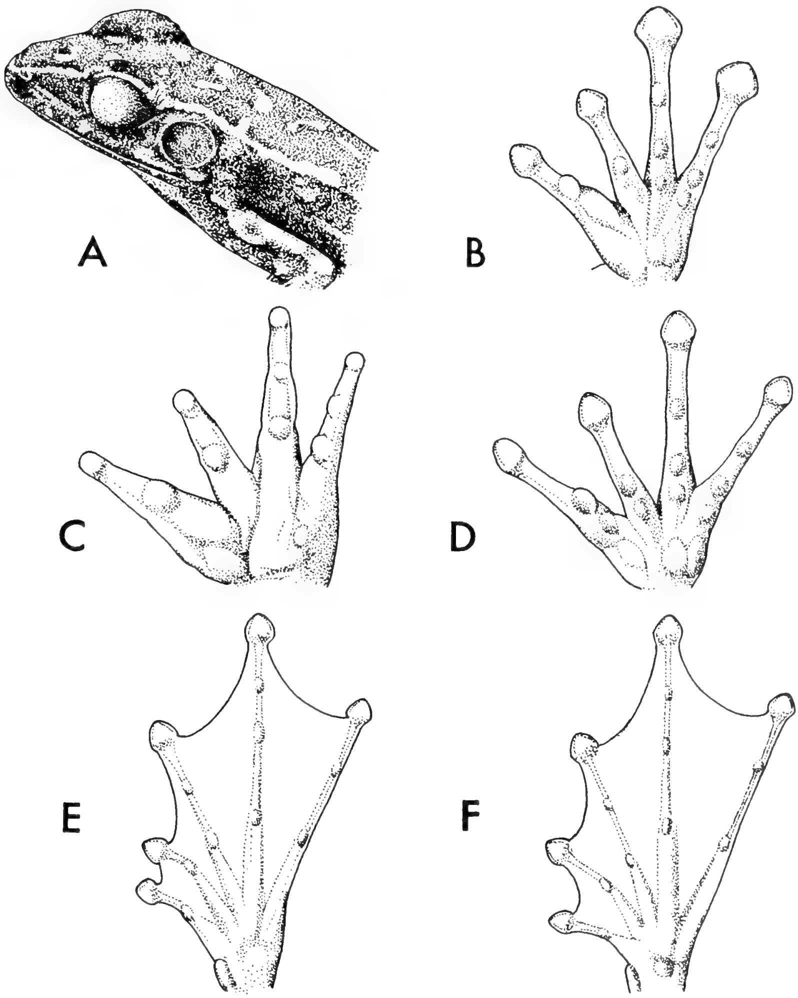


FIG. 30. Key to species of *Rana*.

6A. All toes usually broadly webbed to disks; a freely movable flap of skin on outer edge of fifth toe and metatarsal. . . . . *kuhli*.
B. Toes not fully webbed to disks; no freely movable flap of skin along fifth toe *laticeps*.

7A. Tips of toes distinctly expanded into large or small disks (fig. 30I) . . . . . . 9.
B. Tips of toes blunt or pointed, not expanded (fig. 30J, K). . . . . 8.

8A. Web usually not extending beyond middle tubercle of fourth toe (fig. 30K) *limnocharis*.

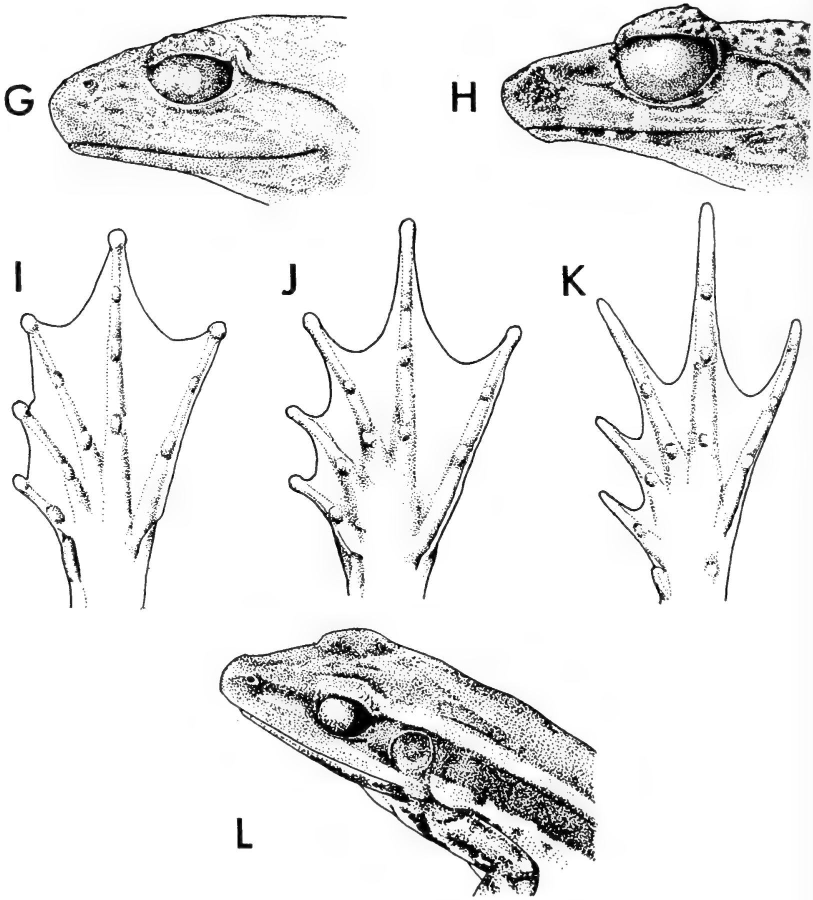


FIG. 30. (cont.) Key to species of *Rana*.

B. Web usually reaching outermost tubercle of fourth toe (fig. 30J) . . *cancrivora*.

9A. A light line or stripe on canthus from tip to eye (fig. 30A) . . . . *signata*.

B. Canthus without light stripe . . . . 10.

10A. A broad, light, dorsolateral stripe beginning behind eye (fig. 30L) . . *erythraea*.

B. Without broad, light, dorsolateral stripes . . . . 11.

11A. Foot with an outer metatarsal tubercle (fig. 30F) . . . . 12.

B. No outer metatarsal tubercle (fig. 30E) . . . . 14.

12A. Upper lip distinctly lighter than cheek, without dark crossbars or spots *nicobariensis*.

B. Upper lip with dark crossbars or light and dark areas . . . . 13.

13A. Web extending well beyond outer tubercle of fifth toe (fig. 36A) . . *glandulosa*.

B. Web extending little (if at all) beyond outer tubercle of fifth toe (fig. 36B) *baramica*.

14A. A dark temporal spot covering entire tympanum (fig. 47)....*paramacrodon*.
B. Dark temporal spot, if present, not covering entire tympanum..........15.

15A. Web reaching disk of fourth toe only as a narrow fringe (as in fig. 30M) *microdisca*.
B. Web reaching disk of fourth toe as a broad sheet (fig. 30N)........... 16.

16A. Third finger with a movable flap of skin on both sides (fig. 30O)..*ibanorum*.
B. Third finger without movable flaps; some frogs with thick, narrow ridges (fig. 30P)..17.

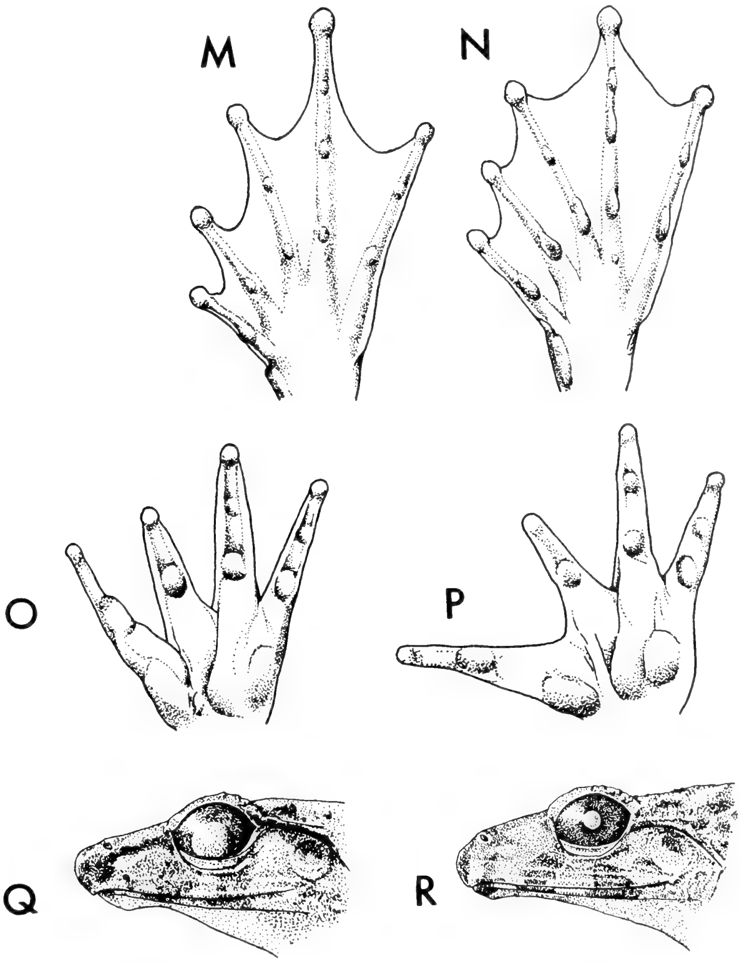


FIG. 30. (cont.) Key to species of *Rana*.

17A. A dark stripe from eye to nostril iust below canthus (fig. 30Q) .... *blythi*.
B. No stripe below canthus (fig. 30R) .... *macrodon*.

KEY TO KNOWN TADPOLES OF BORNEAN SPECIES OF *Rana*.

1A. Lower lip with four rows of teeth .... 2.
B. Lower lip with three or fewer rows of teeth .... 3.

2A. Three to five papillae of lower lip several times length of others.... *luctuosa*.
B. Papillae uniform in length .... *hosei*.

3A. Upper lip with more than one divided tooth row (figs. 35, 48); body with large glandular patches .... 4.
B. Upper lip with one or no divided tooth row; no glandular patches on body 5.

4A. Color greenish or yellowish with black markings on head .... *chalconota*.
B. Color blackish, older tadpoles with light spots on head .... *signata*.

5A. Lower lip with three undivided tooth rows .... 6.
B. Lower lip with one or two undivided rows of teeth; innermost row often narrowly divided .... 7.

6A. Outermost row of teeth on lower lip at least two-thirds of middle row *cancrivora*.
B. Outermost row of teeth on lower lip about half length of middle row *limnocharis*.

7A. Lower lip with only two rows of teeth .... *erythraea*.
B. Lower lip with three rows of teeth ....8.

8A. Papillae of lower lip in two distinct lengths (fig. 46) .... *nicobariensis*.
B. Papillae of lower lip uniform in length .... 9.

9A. Tail abruptly tapered near end followed by a narrow, drawn out tip *microdisca*.
B. Tail gradually tapered in posterior third ....10.

10A. Upper lip with one row of teeth .... *blythi*.
B. Upper lip with two rows of teeth ....11.

11A. Large black spots about half diameter of eye on tail fins .... *kuhli*.
B. No spots larger than one-third diameter of eye on tail fins .... *ibanorum*.

Rana Linnaeus

Rana baramica Boettger

Rana baramica Boettger, 1901, Abh. Senck. Naturf. Ges., **25**, p. 391—Baram River, Sarawak; Boulenger, 1920, Rec. Indian Mus., **20**, p. 182; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 195.

Rana laterimaculata Barbour and Noble, 1916, Proc. New England Zool. Club, **6**, p. 21, fig. 3—Sadong, Sarawak.

Material examined.—Borneo 43 (2 BM; 1 Bogor Mus.; 24 FMNH; 1 MCZ, type of *laterimaculata*; 3 NHMW; 9 SM; 2 SNG, types of *baramica*; 1 ZMA); Bangka 1 (ZMA); Singapore 3 (BM).

Taxonomic notes.—The holotype of *laterimaculata* does not differ from *baramica* in any character.

See further comments under *glandulosa* (p. 185).

Description.—Body stout to slender, legs slender; adults 40–67 mm.; head obtusely pointed, width 0.30–0.34, length 0.37–0.39 of snout-vent; snout longer than eye, projecting slightly in profile; nostril much nearer to tip of snout than to eye; interorbital equal to or wider than upper eyelid; tympanum conspicuous, ⅔ to ¾ eye diameter; vomerine teeth in oblique groups, usually between posterior halves of choanae, groups separated from each other by more than length of one group, closer to choanae.

Tips of finger slightly dilated, with interrupted circummarginal grooves; fingers long, first longer than second; fingers without fringes or flaps of skin; a supernumerary tubercle on all metacarpals. Tips of toes (fig. 36B) like those of fingers; first, second, third, and fifth toes with two phalanges free of web, fourth with 3½ to 3⅔ free; an oval inner and a smaller, round outer metatarsal tubercle; tibia 0.47–0.55 of snout-vent.

Skin shagreened above with small, low glands; an interrupted, weak dorsolateral fold usually visible; sides with scattered oval glands; venter weakly rugose posteriorly, smooth anteriorly, or smooth throughout; a weak supratympanic fold from eye to axilla.

Color (in alcohol) dark brown above, lighter on sides; dark spots scattered on back and sides; venter cream-colored, more or less heavily spotted with dark brown; limbs with dark crossbars dorsally.

TABLE 20.—Sex dimorphism in body proportions of *Rana baramica*. Ratios given in terms of thousandths of snout-vent.

	No.	Range	Median	Comparison of sexes U*	P
			Tympanum diameter		
Males	7	80–98	94		
Females	10	70–91	77	5.5	0.003
			Tibia length		
Males	7	458–480	474		
Females	9	472–554	509	4	0.001
			Head width		
Males	7	301–323	314		
Females	8	302–339	314	22	0.27

* U of Mann-Whitney test.

Secondary sex characters.—Females are larger than males; seven females containing enlarged ova measure 44.3–66.9 (mean 57.30 ± 2.95 mm.) and nine males with vocal sacs 38.9–45.6 (mean 42.81 ± 0.62 mm.). Males have relatively larger tympana and relatively shorter tibias (Table 20). There is no sex dimorphism in head width.

Males have paired subgular vocal sacs having a round opening on each side of the floor of the mouth. The skin overlying the vocal sacs is rugose at each corner of the throat and darker than the adjacent gular areas. The nuptial pad consists of two grayish velvety clusters on the first finger, one an elongated oval on the dorsomedial aspects of the distal half of the metacarpal and the other a small oval on the medial surface of the prepollex. A conspicuous humeral gland, 2.5 mm. long in a male of 42.0 mm., occupies the middle third of the upper arm. Males also have small whitish asperities in the posterior half of the back.

Ecological notes.—Enlarged (1.0–1.5 mm.) and probably mature ova lack pigment, suggesting reproductive habits similar to those of *glandulosa* but differing from the usual *Rana* pattern. All eight specimens for which precise information is available were collected in primary forest. All known localities are within 300 meters of sea level.

Range.—Borneo, Singapore, and Bangka.

SABAH: Sipitang District, Sipitang. SARAWAK: First Division, Kuching, Sadong; Second Division, Engkili; Fourth Division, Baram River, Niah. KALIMANTAN: Semberrah River, Mentawir.

Rana blythi Boulenger. Figure 31.

Rana macrodon var. *blythi* Boulenger, 1920, Rec. Indian Mus., **20**, p. 43 (no type locality given).

Rana blythi Taylor, 1962, Univ. Kansas Sci. Bull., **43**, p. 386, figs. 37-8.

Rana macrodon (non Duméril and Bibron), Flower, 1896, Proc. Zool. Soc. London, **1896**, p. 898 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 174 (part); Smith, 1930, Bull. Raffles Mus., no. 3, p. 98 (part); Inger, 1958, Fieldiana, Zool., **39**, p. 253.

Rana macrodon var. *leporina* Andersson, 1923, Meddel. Zool. Mus. Kristiania, **7**, p. 123—Tumbang Maruwei, Borneo.

Rana macrodon macrodon (part) Inger, 1954, Fieldiana, Zool., **33**, p. 275; 1956, *ibid.*, **34**, p. 402.

Material examined.—Borneo 1083 (5 BM; 1037 FMNH; 2 NHMW; 4 NSH; 8 RMNH; 19 SM; 3 SNM; 5 ZMA); Malaya 104 (79 FMNH; 9 JRH; 16 SNM); Sumatra 3 (NMB).

Taxonomic notes.—Blanford (1881) called attention to two types of *macrodon* in Malaya: a broad-headed type on Singapore and a

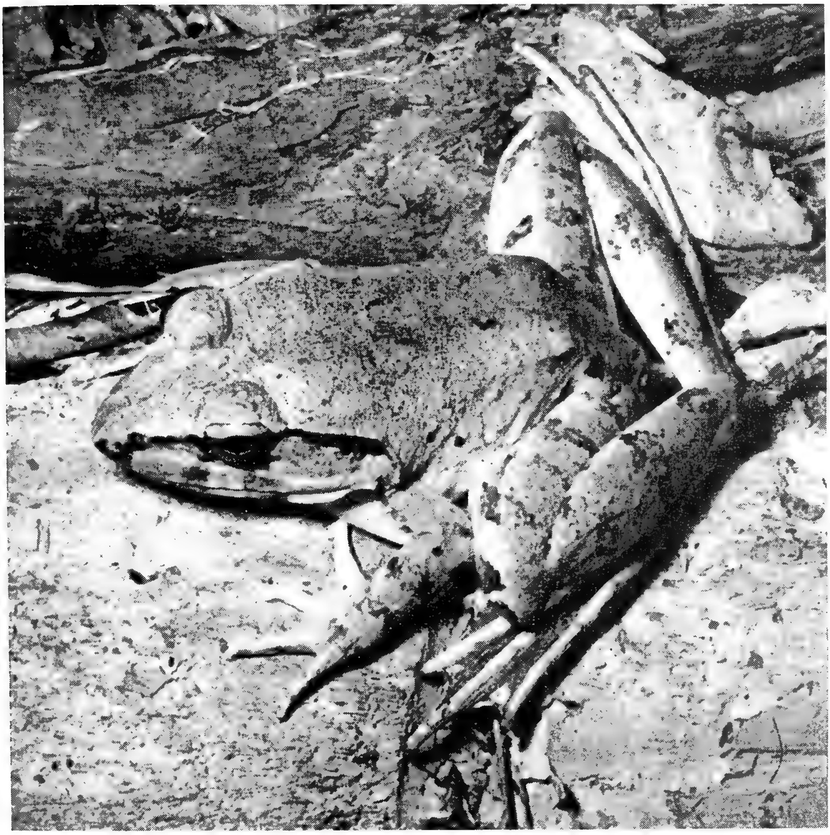


FIG. 31. *Rana blythi*, adult male.

narrow-headed type on Penang Island. The two types also differed in the size of the eye and of the tympanum, and in the fullness of the web. Flower (1896), who had a series from both places, confirmed Blanford's observations. Blanford had noted that the supratympanic fold had a sharp angle in the Singapore variety but a smooth curve in the Penang form. Flower observed a gradation between these two extremes.

The narrow-headed Penang form was described by Boulenger (1920) as the "variety" *blythi*, which according to him differed from typical *macrodon* in having a narrower head, a larger eye, a sharper canthus rostralis, steeper lores, and slightly longer legs. However, Boulenger came to the same conclusion as had Flower, namely, that *blythi* was poorly defined because of the complete gradation between

extreme condition of all characters. Van Kampen (1923) did not recognize *blythi* even as a "variety." Smith (1930), after noting that specimens of "*macrodon*" from the northern part of the Malay Peninsula had narrower heads, larger eyes, and longer legs than those from the southern part of the peninsula, agreed with Boulenger's rejection of *blythi* as a valid form because "the characters . . . do not coincide with any definite geographical distribution. . . ."

Sixty-nine adults from Malaya were examined. All except two were over 90 mm., snout to vent. The two exceptions were females containing mature ova and measuring 80.0 and 81.2 mm. These 69 adults fall into the groups recognized by Blanford and Boulenger: a wide-headed, short-legged frog with an indistinct canthus and sloping lores; and a narrow-headed, long-legged frog with a sharp canthus and steeper lores. Adult males of the first group, which represents true *macrodon*, have tibia to snout-vent ratios of 0.417 to 0.495 (median 0.459; N = 6). Males of the other group, i.e., *blythi*, have tibia ratios of 0.484 to 0.578 (median 0.539; N = 26); in only three does the ratio fall below 0.5. Females show the same divergence: in three *macrodon* females the ratio is 0.450–0.461 (median 0.459) and in 27 of *blythi* the ratio is 0.488–0.577 (median 0.539). In only one *blythi* female is the ratio less than 0.5.

The ratio of head width (at the level of the tympanum) to snout-vent varies from 0.429 to 0.467 (median 0.462) in seven male *macrodon*, and from 0.344 to 0.427 (median 0.369) in 24 *blythi* males. The three adult *macrodon* females had head-width ratios of 0.336, 0.400, and 0.441. In 26 *blythi* females this ratio had a range of 0.320–0.385 (median 0.354).

The web is slightly fuller in the narrow-headed, long-legged *blythi* frogs. Although the web reaches the base of the swollen tip of every toe in both forms, it is more deeply excised in *macrodon*. When the fourth and fifth toes are brought together, the edge of the narrowest part of the interdigital membrane is approximately at the level of the middle subarticular tubercle of the fourth toe. The margin of the web is even with the proximal edge of that tubercle in eight of the 10 *macrodon* adults and even with the distal edge of the tubercle in the other two. In Malayan *blythi* adults, the margin of the web reaches the level of the proximal edge of the tubercle in 11, the center of the tubercle in 25, and the distal edge of the tubercle or beyond in 18. The difference between these distributions is statistically significant (chi-square = 15.21, degrees of freedom = 2; P = 0.001).

The difference in the shape of the supratympanic fold noted by Blanford is partly borne out by my specimens. But the value of this character in distinguishing the two forms is reduced by the gradation between the extremes observed by Flower (1896) and by the difficulty of making reasonably accurate measurements. Because of the latter difficulty, I have not checked the presumed difference between eye sizes.

Another difference lies in the color of mature ova. In the wide-headed, short-legged *macrodon*, a mature egg has a black hemisphere and a light one; it is a typical *Rana* egg. In *blythi*, however, the eggs are entirely light yellowish gray.

The seven adults seen from Java (the type locality of *macrodon*) all belong to *macrodon* proper. Their heads are wide with obscure canthi and sloping lores, and their legs are short (tibia ratio 0.432–

TABLE 21.—Comparison of body proportions of adult (snout-vent greater than 90 mm.) *Rana macrodon* and *R. blythi* from Borneo. Values of proportions given in terms of thousandths of snout-vent length.

	Range	Median	N	Z*	P*
	Head width at level of tympanum				
Males					
blythi	338–400	378	24	1.989	0.046
macrodon	376–444	399	14		
Females					
blythi	334–364	352	11	3.357	0.001
macrodon	344–416	376	15		
	Head width immediately before eye				
Males					
blythi	214–246	232	25	4.951	<0.001
macrodon	241–274	254	14		
Females					
blythi	206–241	228	14	4.140	<0.001
macrodon	229–276	246	15		
	Tibia length				
Males					
blythi	521–615	564	27	4.294	<0.001
macrodon	499–562	527	15		
Females					
blythi	515–616	588	19	3.887	<0.001
macrodon	453–561	504	12		

* As calculated from the Mann-Whitney U test; Z gives the single tailed distribution under the normal curve. P in this table has been multiplied by 2.

0.513). Only one of the two females has enlarged ova and they are bicolored as in Malayan *macrodon*.

Flower (1896) and Boulenger (1920) reported both *blythi* and *macrodon* from Borneo. In two papers (Inger, 1954A, 1958) discussing these Bornean frogs, I failed to distinguish between them. Andersson (1923) described the Bornean "variety," *leporina*, noting that its legs were longer than those of true *macrodon*. Taylor (1962) notes that the two forms, *blythi* and *macrodon*, occur together and should not be treated as subspecies.

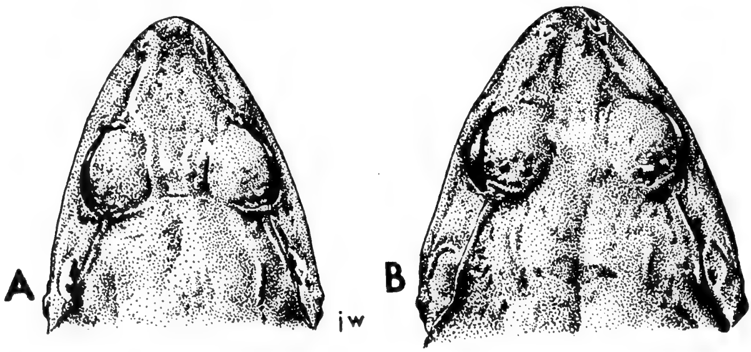


FIG. 32. Dorsal views of heads of *Rana blythi* (A), and *R. macrodon* (B).

In Borneo two species exist and occur together in some places. One fits Boulenger's definition of *macrodon* and the other his description of *blythi*. Adults (snout-vent 90 mm. or more) of the two are easily distinguished by the shape of the head (Table 21). The broad-headed form (fig. 32B) has a very feebly defined canthus and lores so oblique as to be almost horizontal. Its head is exactly like Blanford's (1881) figure of the broad-headed Singapore form. The narrow-headed Bornean frog (fig. 32A) has a sharply angular canthus and steep, almost vertical lores, which are deeply concave. Adults from Borneo show no intergradation in these aspects of head shape. The same differences are evident in juveniles though their heads are relatively less wide.

The two groups of Bornean frogs separated on the basis of head shape differ just as the corresponding forms in Malaya do: the broad-headed one, *macrodon*, has shorter legs (Table 21), less extensive webbing (Table 22), and pigmented ova; the narrow-headed one has longer legs, fuller webbing and non-pigmented ova.

TABLE 22.—Extent of interdigital membrane between fourth and fifth toes in Bornean *Rana macrodon* and *R. blythi*. Explanation in text.

	Proximal edge of tubercle	Center of tubercle	Distal edge of tubercle or beyond
		Number of individuals	
Rana macrodon	27	15	0
Rana blythi	1	5	65

Other differences not found in Malayan samples distinguish the Bornean populations. The narrow-headed *blythi* has a dark horizontal loreal stripe just below the canthus. The stripe is especially conspicuous in juveniles and is visible in most adults although it becomes somewhat obscured. A loreal stripe does not appear in Bornean *macrodon* of any size.

A mid-dorsal light band or line appears in *macrodon* (5 of 12) and *blythi* (25 of 104) of Malaya. Thirteen per cent of 291 Bornean *macrodon* have a similar marking, but none of the hundreds of Bornean *blythi* do.

As stated, the two forms have been collected together at a number of localities in Borneo: at three localities within 65 km. of Sandakan, Sabah; at Nanga Tekalit, Third Division, Sarawak; and at Labang and Sungei Pesu, Fourth Division, Sarawak. In a number of instances frogs of these two forms were caught within 10 meters of each other. Both have been caught on Singapore Island.

The distinctive characters of one form (e.g., *macrodon*) cannot be thought of as the chance products of a single mating because Bornean *macrodon* at hand were collected in 1928, 1950, 1956, 1957, 1962, and 1963 and from localities in Borneo spread over 700 kilometers. The Bornean *blythi* available were obtained from 1950 to 1963 and from localities also scattered over 700 kilometers. The assumption of genetic and developmental independence of the characters in which these two forms differ is reasonable; in fact, the reverse assumption of genetic or developmental interrelationship of egg pigmentation, slope of the lores, and extent of webbing is so improbable as to be practically insupportable. The only explanation for the existence of two forms differing in a number of genetically independent characters and occurring sympatrically over such a great distance is that two distinct species are involved.

Sympatry of such similar species raises the question of isolating mechanisms. Unlike most species of *Rana*, *blythi* and *macrodon* (at least the Bornean populations) have no breeding call. Consequently

reproductive isolation cannot be maintained by call differentiation. Differences in habitat selection probably do not isolate them. All of the Bornean frogs for which I have detailed notes—i.e., the majority of specimens examined—were caught on the banks of small streams or large rivers. On small streams *macrodon* showed a greater tendency to be concentrated near the mouths than does *blythi*. *Rana macrodon* was commonly caught in logged rain forest, in secondary growth, or in clearings surrounded by forest; only rarely was it caught in primary forest. *Rana blythi* occurs in similar places and is especially abundant in primary forest. At Nanga Tekalit, Sarawak, for example, the ratio of individuals caught in primary as opposed to those caught in logged forest was 1:3.1 in *macrodon* and 1:1.4 in *blythi*. At Sepilok Forest Reserve, Sabah, one *blythi* was collected in virgin forest and two in the modified habitats; the 22 *macrodon* from Sepilok were all caught in modified habitats. At Bukit Kretam two *blythi* were caught in undisturbed primary forest and two *macrodon* in clearings. At Sapagaya Forest Reserve four *blythi* were collected in primary forest and seven in logged forest; two *macrodon* were caught in the same logged forest. At Kalabakan 40 *blythi* and no *macrodon* were collected in primary forest. At Deramakot, where logging operations were just beginning in 1956, only *blythi* was found. On the other hand, in the modified environments around Sandakan—rubber plantations, secondary growth, etc.—only *macrodon* has been collected.

The difference between *blythi* and *macrodon* in relative abundance in modified and in undisturbed climax vegetation may not be simply a matter of ecological differentiation and isolation. Instead this difference may be a consequence of the fact that *macrodon* is probably a recent invader of Borneo and has not had time to occupy the pristine forests (see below).

The only two individuals of *blythi* now known from Singapore Island were caught in forest on the top of Bukit Timah (160 meters above sea level), which has until now been relatively undisturbed. *Rana macrodon* has been caught just a few kilometers away at Nee Soon, an area of secondary forest. Farther north *macrodon* has been collected at Selinsing, Perak, along the heavily populated western coast of Malaya. It is not known from primary forest in the interior of the peninsula. *Rana blythi* has been caught in the forest of King George V National Park in the interior of Pahang.

The breeding habits of these species may differ. This tentative conclusion is indicated by the difference in egg pigmentation (see

above) though it does not confirm it. No positive, direct evidence exists. However, the bicolored eggs of *macrodon* suggest the typical ranid habit of oviposition in exposed aquatic sites. The light, unicolor eggs of *blythi* suggest a departure from that pattern as non-pigmented eggs are usually associated with peculiarities in sites of oviposition. (See also under *Ecological notes,* below.)

The mode and mechanisms of isolation of these two species are still uncertain and merit additional work.

As noted above, the distributions of these species imply that *macrodon* has not been in Borneo as long as *blythi*. *Rana blythi* occurs the length and breadth of Borneo (see *Range* below) and does not live in greatly disturbed vegetation. *Rana macrodon,* on the other hand, lives in situations that are geographically and often ecologically peripheral. Coastal clearings and strongly modified environments, such as rubber plantations, where *macrodon* is abundant, are the work of man and therefore younger than the primary forests. The absence of *macrodon* from interior forests, such as that at Deramakot, Sabah in 1956, suggests that it simply has not had time to reach those areas. In 1956 *blythi* but not *macrodon* was collected at several places in the Baleh River basin, Sarawak. In 1962 *macrodon* as well as *blythi* were caught in the Baleh basin in the same general area and in the same kinds of environments worked in 1956. The conclusion seems inescapable that *blythi* has been in Borneo a long time and that *macrodon* is a recent arrival.

In Malaya the two species have analogous distributions: *macrodon* is found only in modified coastal areas, whereas *blythi* is abundant in interior primary forest as well as near the coast. Therefore, *macrodon* is probably the more recent arrival in Malaya also. Known Malayan localities are Singapore Island and coastal Perak.

Both species occur in Sumatra; the five specimens seen (two are *macrodon*) are from coastal areas. All seven of the Javan frogs seen are *macrodon*; the two with definite locality data are from Garut in the interior. If only *macrodon* lives in Java, then probably *macrodon* originated in Java and has recently spread westward into Malaya and northward into Borneo.

Description.—Body stocky; limbs heavy, long (tibia 0.52–0.62 of snout-vent); snout-vent to well over 150 mm.; head longer than broad; snout pointed; canthus rostralis distinct, acute; lores almost vertical, deeply concave; tympanum always visible; vomerine teeth in two large, oblique groups beginning near the anteromedian corners of choanae, the groups narrowly separated; lower jaw with a pair of

bony projections near symphysis; skin of back smooth in adults, juveniles with scattered round tubercles and an inverted V-shaped ridge between shoulders; a strong temporal fold; no dorsolateral fold.

Fingers bluntly rounded; first longer than second; no supernumerary metacarpal tubercles; distinct ridges (not flaps) of skin along inner edges of second and third fingers; tips of toes expanded into round disks lacking grooves; web reaching disks of all toes as a broad sheet (Table 22); movable flaps of skin on outer edge of fifth toe and on inner edge of first; subarticular tubercles oval; inner metatarsal tubercle oval, shorter than first toe; no outer metatarsal tubercle.

Color (in life) light chocolate brown to red, juveniles with dark markings on back; a straight interorbital black bar; lips with broad black bars; a narrow, black loreal stripe between nostril and eye; a black stripe from eye across upper half of tympanum; limbs with dark crossbars; underside pale creamy white; throat usually faintly mottled with black; chest unspotted; underside of web black. Bornean specimens without light mid-dorsal line or band.

Secondary sex characters.—Males of *blythi* do not have vocal sacs, nuptial pads, or other distinctive structures. However, males (often confused in literature with *macrodon*) have long been known to have decidedly larger heads than do females (Boulenger, 1920). This enlargement involves both width and length. The ratio of head length to snout-vent in 25 adult Bornean males varies from 0.390 to 0.483 (median 0.446), those of 15 females from 0.391 to 0.440 (median 0.409); data for head width ratios are given in Table 21. The differences between the sexes in both ratios are statistically significant at the 0.001 level (using the Mann-Whitney U test).

Change in head length is effected primarily behind the eye as in the closely related Philippine frog, *Rana magna* (Inger, 1954A). Enlargement of the bony mandibular projections into long tooth-like structures in the males is undoubtedly part of the same growth pattern.

In this species and in its Bornean relatives, *macrodon, kuhli, ibanorum,* and *paramacrodon,* absence of vocal sacs is accompanied by loss of voice. None of the hundreds of males of these species observed were calling, though the collection of ripe females and larvae of all species (except *macrodon*) during the same interval indicates that the observations were made during the breeding season when males would have been expected to call.

Sexual maturity is attained when the frogs reach 85–90 mm. Of 21 females in the size range 85–89 mm., 11 have mature oviducts (en-

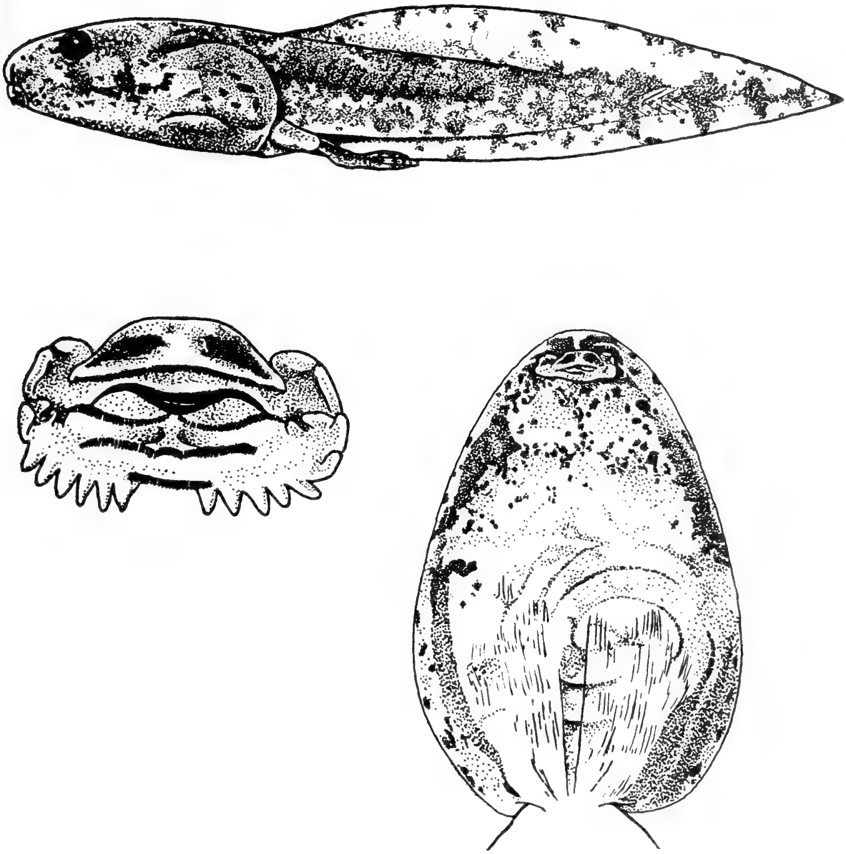


FIG. 33. Tadpole of *Rana blythi* from Sarawak.

larged and strongly convoluted) and 10 have immature ones; only three of the 37 females in the 90–94 mm. range have immature oviducts, whereas only three of 21 in the 80–84 mm. class have mature ones. The characteristic enlargement of the head becomes apparent in males at about 90 mm.

Larvae.—Body oval (fig. 33), width about three-fourths body length, somewhat flattened above, eyes and nostrils dorsal; interorbital and internarial distances equal to nostril-snout but greater than eye-nostril distances; oral disk ventral, subterminal; disk about one-third width of head, width less than interorbital; upper lip very short, bordered by a continuous row of teeth; thick papillae in a single row at lateral corners of upper lip and continuous except for

a narrow median gap along lower lip; one to three papillae forming a second row laterally on the lower lip of a few individuals; labial teeth uniformly I/1–1:II (35 counted), the outermost row of the lower lip between one-third and one-half the two inner ones, which equal the row of the upper lip; all labial teeth rather weak; beaks very feebly serrated, black in distal third.

Spiracle sinistral, tubular, midway between eye and root of hind-limbs and on a line connecting those points; anus dextral, opening at edge of ventral fin from a tube longer than eye diameter in a Stage VIII larva.

Tail strong, obtusely pointed, both edges similarly convex, maximum depth in proximal third, depth about 0.15 of total length; dorsal fin not as deep as caudal muscle but slightly deeper than ventral fin.

Color (in alcohol) of body mottled pale brown with blackish brown, the dark pigment in a streak sloping downward and forward from the eye, a vertical bar below the center of the eye, and a vertical bar behind the eye; an obscured bar across the root of the tail; caudal muscle heavily mottled or barred with black; both fins spotted or barred with black, especially posteriorly; ventral surface of body usually colorless except for small spots in area around oral disk.

The series extends from Stage VIII (foot paddle) to Stage XXII (fore limbs erupted, mouth to below center of eye). Body, total length (mm.), and number of specimens measured for each stage (Taylor and Kollros, 1946) follow.

Stage	No.	Body	Total length
VIII	2	9.4–10.0	28.2–28.8
XI	1	12.2	37.4
XIII	4	11.0–12.2	33.7–36.6
XIV	3	11.4–12.7	35.5–38.5
XX	1	9.5	27.0
XXII	1	10.9	18.1

Two completely metamorphosed frogs (FMNH 139550) measure 9.0 and 11.1 mm.

The almost complete developmental series permits virtually certain identification of these tadpoles as either *blythi* or *macrodon*. Their diagnostic characters are: fully webbed toes, relatively short fourth toes, flap of skin on the outer edge of the fifth toes, oval but not elongate subarticular tubercles, and absence of flaps of skin on the fingers. The last two characters distinguish *blythi* and *macrodon* from *ibanorum* and *kuhli*.

The metamorphosing frog (Stage XXII) has a dark canthal streak, which differentiates *blythi* from *macrodon.* At Kalabakan where some of the larvae were caught, no adults or juveniles of *macrodon* were seen.

Bornean larvae previously ascribed to this species (Inger, 1956; under the name *macrodon*) are clearly those of *Rana microdisca finchi.*

The larvae described from Penang by Flower (1899) under the name *macrodon* differ from those described above in the following ways:

labial teeth:

Flower's tadpole	I:1–1/1–1:II
Bornean *blythi*	I/1–1:II

tail shape:

Flower's tadpoles	acutely pointed, attenuate
Bornean *blythi*	rounded at tip, not attenuate

Ecological notes.—*Rana blythi* is one of the most abundant amphibians along the rivers and streams of the Bornean rain forest. The stream may be large or small, shallow or deep, clear or muddy. Although *blythi* appears to be much more abundant in primary forest, it also occurs in secondary growth, particularly where trees partially shade the stream (see *Taxonomic notes* above).

Adult frogs are usually seen on banks and are equally common on mud, gravel, or rock substrates. Juveniles may be found a short distance from the banks, but we encountered no adults farther than 10 meters from the water's edge. However, adults do not rest in the water, as does *kuhli* for example, except when frightened.

Larvae have been collected in both clear and muddy streams in shallow pools generally separated from the main current by sand and gravel bars. These pools usually have an accumulation of dead leaves on the bottom. The tadpoles graze over the surface of these leaves. Diatoms, green algae, blue-green algae, fragments of higher plant epithelium, and fine sand grains appear in smears made from the intestines of larvae.

Females having enlarged eggs were captured in all months of the year in Sarawak. Breeding activity seems to be continuous. During a full year of observation, our field party caught no adults in amplexus or ovipositing. The Ibans who worked for us insisted that *blythi* excavates shallow nests in wet gravel spits. On one occasion our

party saw two adult *blythi* in a shallow depression (ca. 20×5 cm.) in a gravel bar. Unfortunately, the frogs were disturbed and leapt away.

This supposed breeding site makes sense ecologically. The interstices of these sand and gravel bars are always filled with water and generally a shallow pool such as the tadpoles live in is partly cut off from the main current by the bar. Larvae could hatch and wriggle through the shallow layer of gravel to the protected pool.

In Borneo *blythi* is common at low elevations, occurring in numbers within a few feet of sea level, but is apparently less abundant above 300 meters. The highest Bornean elevation from which correctly identified specimens are known is 1000 meters (Pa Main, Kelabit Plateau).

Geographic variation.—The Bornean samples of *blythi* show no geographic variation in the characters analyzed. For this reason they are lumped in the following comparisons.

Bornean specimens have no light mid-dorsal marking and no light line on the dorsal surfaces of the leg. Twenty-five of the 104 Malayan frogs seen have a light vertebral line or band, only one has a light line dorsally on the leg. The black loreal stripe characterizing all of the Bornean frogs (p. 170) is present in only one Malayan specimen and is absent in all three from Sumatra.

The web is generally more extensive in the Bornean samples although the range of variation is the same as in the Malayan population. Using the method of measurement outlined above (p. 164), the web reaches the distal edge of the subarticular tubercle of the fourth toe (or beyond) in 86 Bornean frogs, the center of the tubercle in five, and the proximal edge of the tubercle in one. Comparable frequencies for the Malayan sample are 18, 25, and 11.

Bornean specimens have longer legs than do Malayan *blythi*. The ratio of tibia to snout-vent for males of the Bornean sample varies from 0.521 to 0.615 (median 0.564; $N=27$); for males from Malaya the corresponding figures are 0.484–0.578 (median 0.539; $N=26$). The difference between these samples is statistically significant at the 0.001 level (Mann-Whitney U test: $Z=3.860$). For Bornean females the tibia ratio has a range of 0.515–0.616 (median 0.584; $N=19$); Malayan females have a range of 0.488–0.577 (median 0.538; $N=27$). The difference between the two samples of females is statistically significant at the 0.001 level ($Z=4.451$). Males of the two populations differ in the ratio of head length to snout-vent. In the Bornean sample the range of this ratio is 0.390–0.483 (median 0.446;

N = 25) and in the Malayan one is 0.388–0.485 (median 0.426; N = 25); Z = 2.328, P = 0.02.

Range.—At present the species is known with certainty from Malaya as far north as Kaki Bukit, Perlis (SNM, unnumbered—6°39′N), Borneo, and Sumatra.

SABAH: Jesselton District, Menggatal; Kinabatangan District, Bukit Kretam, Deramakot; Kudat District, Bongon; Lahad Datu District, Sungei Pangaruan; Ranau District, Ranau; Sandakan District, Betotan, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tawau District, Brantian River Estate, Kalabakan. SARAWAK: First Division, Kuching, Bukit Lintang, Matang, Sabar Tabang, Sadong, Samunsam valley; Third Division, Baleh River near mouth of Sungei Putai, Kapit, Mount Dulit, Nanga Tekalit; Fourth Division, Akah River, Labang, Long Peluan, Meligong, Pa Main, Patah River, Sungei Pesu, Tutoh River valley. KALIMANTAN: Balikapapan, Bluu, Long Petah, Nanga Raun, Nunukan Island, Samarinda, Semberrah River basin.

Rana cancrivora cancrivora Gravenhorst

Rana cancrivora Gravenhorst, 1829, Delic. Mus. Zool. Vratisl., **1**, p. 41—Java; Boulenger, 1920, Rec. Indian Mus., **20**, p. 23; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 170.

Rana cancrivora cancrivora Dunn, 1928, Amer. Mus. Novit., no. 315, p. 5; Inger, 1954, Fieldiana, Zool., **33**, p. 260, figs. 49–50; 1956, *ibid.*, **34**, p. 401.

Material examined.—Borneo 138 (10 BM; 112 FMNH; 5 NSH; 2 RMNH; 9 SM); Java 4 (USNM); Singapore 2 (FMNH).

Description.—Body stocky; limbs moderate to heavy; adults 50 to 85 mm.; head as broad as long; snout rounded or obtusely pointed; tympanum visible, one-half to two-thirds eye diameter; irregular skin folds on back; a supratympanic fold from eye to axilla.

Fingers pointed; first longer than second; fingers without fringes of skin. Toes pointed as fingers; web reaching almost to tips of first, second, and third toes on outer border and on inner border of fifth, to middle subarticular tubercle of fourth or slightly farther; a flap of skin on outer edge of fifth toe; an elongate inner but no outer metatarsal tubercle.

Color (in alcohol) gray or brown above with irregular dark markings, often in form of W; limbs with dark crossbars; below whitish, with or without dark mottling.

Secondary sex characters.—Females are larger than males; the range of 19 females was 52.9–82.0 mm. (mean 68.59 ± 2.02) and of

25 males 51.0–70.9 mm. (mean 58.75±0.84). As noted elsewhere (Inger, 1954A), males have median subgular vocal sacs, black patches at the corners of the throat, nuptial pads on the first fingers, and colorless ventral asperities.

Larvae.—Body oval, width about one-third length; eyes dorsal; spiracle lateral, equidistant between base of tail and tip of snout; vent dextral.

Oral disk ventral; single row of papillae laterally on upper lip, two rows on lower lip with a narrow median gap; labial teeth I:1–1/III, outermost row of lower series two-thirds to three-fourths length of second row; beaks edged with black.

Tail less than twice length of body, pointed; length of tail about four times its depth; dorsal fin twice depth of ventral one which is low.

Back and sides dark gray, spotted with darker pigment; advanced stages often with dark interorbital bar. (After Annandule, 1918, and Alcala, 1962.)

Ecological notes.—*Rana cancrivora* is intimately associated with man in Borneo, occurring only along the coast or in the lower reaches of large river basins. It is never found in rain forest but lives in such modified habitats as rubber plantations, roadside ditches, and artificial ponds. All of the known Bornean localities are below 200 meters above sea level.

Females collected in and around Sandakan in April, July, and August contained pigmented ova. Males collected at the same times had well-developed secondary sex characters.

Geographic variation.—As already shown (Inger, 1954A), the Bornean population has a narrower head than do those of Palawan and Mindanao, and a shorter leg than the population of Palawan but a longer one than that of Mindanao.

Range.—From the Malay Peninsula to Flores in the Lesser Sundas and from Java to Luzon.

SABAH: Beaufort District, Padas River; Labuk District, Beluran; Lahad Datu District, Lahad Datu; Sandakan District, Sandakan. SARAWAK: First Division, Kuching, Gunong Ngili, Sadong, Santubong, Temiang; Fourth Division, Baram River (van Kampen, 1923); Fifth Division, Limbang. KALIMANTAN: Bandjermasin, Sebruang River, Singkawang, and Sintang (*ibid.*), Balikpapan, Rantau.

Rana chalconota (Schlegel)

Hyla chalconota (part) Schlegel, 1837, Abbild. Amph., p. 23, pl. 50, fig. 3—Java.

Rana chalconota (part) Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 66, fig.

Material examined.—Java 39 (6 BM; 23+larvae FMNH; 10 RMNH, including 5 cotypes of *chalconota*).

Taxonomic notes.—In the original description of *Rana labialis*, Boulenger (1887A) did not state exactly how it differed from *chalconota*. Later Boulenger (1920) placed *labialis* in the synonymy of *chalconota*. Van Kampen (1923), however, maintained that *labialis* differed from *chalconota* in the size and shape of digital disks and in the width of the dorsolateral fold, and that *labialis* should be considered a distinct species. Smith (1930) followed Boulenger's last opinion. Although I previously (Inger, 1956) followed Boulenger and Smith, examination of types of both forms and larger series from Borneo, Java, and Malaya convinces me that my earlier opinion must be modified.

Although the differences between these two frogs in the digital disks and dorsolateral glandular folds are difficult to measure and describe, comparison of series from Malaya and Java bear out van Kampen's observations. In addition to these differences, these forms differ in the coloration of the upper lip, in the masculine secondary sex characters, and in larval characters. These differences, which are discussed in detail under *Geographic variation*, are sufficient for the recognition of distinct subspecies. The two forms are much too similar to be treated as full species; they resemble one another more than do sympatric species of *Rana* in Malaysia. This view is at odds with that of van Kampen (1923), who called them full species and reported both from Borneo and Sumatra.

Five specimens from Sumatra (listed in *Material examined* of *raniceps*) are in poor condition, making their allocation difficult. They have the large finger disks and labial coloration of *chalconota raniceps*.

Rana chalconota raniceps (Peters)

Polypedates raniceps Peters, 1871, Monatsber. Akad. Wiss. Berlin, **1871**, p. 580—Sarawak; 1872, Ann. Mus. Civ. Genova, **3**, p. 44, pl. 6, fig. 3.

Rana chalconota Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 66 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 217 (part); Smith, 1925, Sarawak Mus. Jour., **3**, p. 33; 1931, Bull. Raffles Mus., no. 5, p. 17; Inger, 1956, Fieldiana, Zool., **34**, p. 408.

Rana labialis Boulenger, 1887, Ann. Mag. Nat. Hist., (5), **19**, p. 345, pl. 10, fig. 1—Malacca; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 220.

Material examined.—Borneo 174 (1 BM; 145+18 lots of larvae FMNH; 1 MCG, type of *raniceps*; 1 NHMW; 3 NMB; 1 NSH; 11 RMNH; 11 SM); Malaya 11 (3 BM, cotypes of *labialis*; 8 FMNH); Sumatra 5 (2 FMNH; 3 ZMA).

Taxonomic notes.—The type of *raniceps* is identical to the Bornean frogs referred to in literature as *labialis* and *chalconota*.

Description.—Body and legs slender; adults 33–60 mm.; head triangular, width 0.27–0.33, length 0.37–0.42 of snout-vent; snout

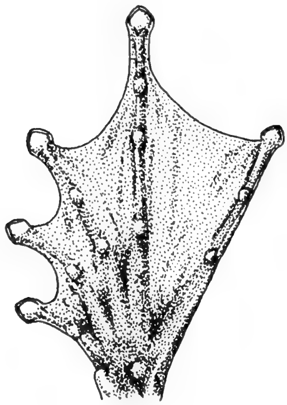


FIG. 34. Ventral view of foot of *Rana chalconota*.

pointed, much longer than eye, not projecting in profile; nostril behind level of symphysis but much nearer to tip of snout than to eye; interorbital equal to or wider than upper eyelid; tympanum conspicuous, two-thirds to three-fourths eye diameter in females, larger in males; vomerine teeth in oblique groups between choanae, groups separated from each other and from choanae by length of one group or less.

Finger tips dilated into disks, that of first finger small, those of outer fingers at least twice width of phalanges and two-thirds the width of tympanum in females; disks with deep horizontal circummarginal grooves; first finger shorter than second; three outer fingers usually with distinct dermal fringes or flaps on both sides; a supernumerary tubercle on each of three outer metacarpals. Tips of toes (fig. 34) with distinct disks, smaller than those of outer fingers; web reaching disks on outer edges of first three toes and on inner edge of fifth toe; fourth toe with one or two phalanges free of broad web; an oval inner metatarsal tubercle and a conspicuous, round outer one; heels overlapping when flexed limbs held perpendicular to body; tibia 0.51–0.60 of snout-vent.

Skin above coarsely shagreened or granular (see also *Secondary sex characters*); dorsolateral glandular fold present, sometimes obscure in preserved frogs; several glands behind rictus; no fold from eye to axilla; skin of posterior half of abdomen coarsely granular or rugose; rest of venter smooth.

Color (in life) pale yellow or yellowish green above, cream-colored below, upper lip white; posterior and ventral surfaces of thigh and ventral surfaces of tibia reddish. In alcohol usually reddish brown above, often with small dark spots; below whitish, dusky spots present or absent; hind limbs with or without dark crossbars.

Secondary sex characters.—Adult females are larger than males. The range of snout-vent in Bornean females is 46.0–59.4 mm. (smallest with mature ova $=46.5$ mm.), and the mean of 38 is 50.68 ± 0.51 mm. Bornean males having vocal sacs range from 32.9 to 44.0 mm. (mean of $55 = 36.73 \pm 0.38$ mm.).

The tympana of males are visibly larger than those of females. The ratio of tympanum diameter to snout-vent length varies from 0.093 to 0.131 (median 0.111) in 42 Bornean males and from 0.067 to 0.087 (median 0.079) in 16 Bornean females. The tibia is also somewhat longer in males, the ratio of tibia to snout-vent having a median value of 0.555 in 41 males and 0.548 in 18 females. Though the range of this character is the same (0.51–0.60) in both sexes, the difference in the distributions is statistically significant (Z of Mann-Whitney test $=3.740$; $P=0.001$).

All Bornean males larger than 32 mm. have paired subgular vocal sacs having round openings in the floor of the mouth. Each of these males also has a linea masculina along the dorsal border of the oblique externus muscle and an oval humeral gland about 2 mm. long. The nuptial pad is a yellowish cluster of fine spinules on the mediodorsal surface of the first finger, extending from the base of the finger to the level of the subarticular tubercle; the pad is constricted at its center in about one-half of the males examined. On the back, each of the dermal granules, which are rounded in females, is surmounted in males by a whitish spinule. Such spinules also occur on the top and sides of the head.

Larvae.—Several hundred larvae (fig. 35) ranging in age from hatchlings to late metamorphic stages were examined. They agree with van Kampen's description (1923) except that the innermost row of lower labial teeth is always interrupted. Van Kampen fails to mention the distinctive pattern on the head.

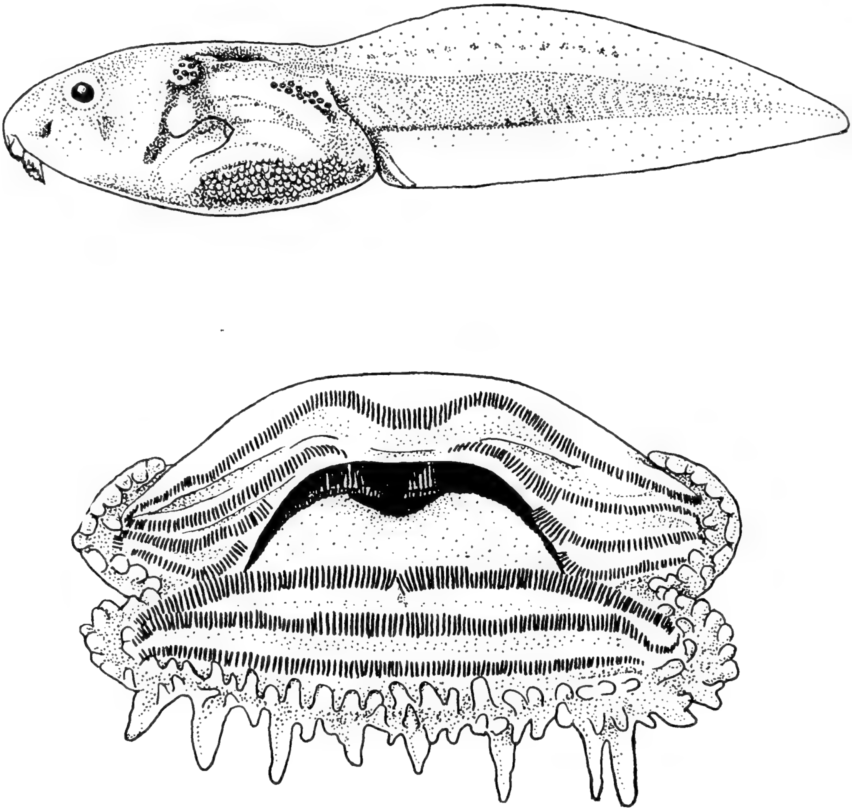


FIG. 35. Tadpole of *Rana chalconota* from Borneo.

Body oval, width about two-thirds length; eyes and nostrils dorsal; eye-nostril distance shorter than internarial distance which is shorter than interorbital distance; oral disk ventral, subterminal, disk about one-half head width; short thick papillae in a continuous series across lower lip and at corners of upper lip; dental formulae in older larvae (beyond Stage I) I:3–3/1–1:II (19), I:3–4/1–1:II (6), or I:4–4/1–1:II (8); beaks finely serrated, black along margin only.

Spiracle sinistral, with very short tube, midway between eye and root of hind limb and on a line between them; anus dextral, tubular, opening at margin of ventral fin.

Tail moderate, tapering gradually to rounded point, about 0.6 of total length; dorsal fin slightly deeper than ventral, deeper than caudal muscle only in distal half.

Body of older larvae with distinct glandular patches; on each side a round temporal patch equal in diameter to interorbital width, an elongate dorsolateral patch running obliquely forward from root of hind limb, an elongate ventrolateral patch running forward from hind limbs, and a small circular patch behind the oral disk.

Color (in alcohol) pale yellowish brown with black markings; a small circular black spot laterally below nostril, a vertical black bar below eye, a curved, vertical black line laterally behind the head, and a roundish black spot dorsolaterally behind head; an interorbital black spot or bar usually present; tail without pigment.

In tadpoles without hind limb buds the labial tooth count in ten (head and body 5.2–5.5 mm.) is I:1–1/1–1:II, in twelve (head and body 5.2–6.9 mm.) I:2–2/1–1:II, and in four (7.6–10.2 mm.) is I:3–3/1–1:II. Of these same larvae, most (5.2–5.5 mm.) have only ventro-lateral glandular patches, two (5.4, 6.9 mm.) have ventro-lateral and temporal patches, and four (7.6–10.2 mm.) have ventro-lateral, temporal, and dorso-lateral glandular patches. Pre-metamorphic larvae (Stages XVI to XIX) have head and body lengths of 12.8 to 18.1 mm.

Ecological notes.—In Borneo adults and larvae of *Rana chalconota* are abundant along small streams both in primary forests and in secondary growth and around swampy areas at the edge of clearings. In such places adults can be observed on muddy or rocky banks or in low vegetation as high as two meters above the ground. I collected approximately equal numbers in primary forest and secondary growth, but never observed *chalcanota* around pools in the center of large clearings or in ditches in towns. In the avoidance of these more exposed situations, it differs sharply from *Rana nicobariensis.*

Tadpoles are usually found in quiet pools of clear streams or in swampy areas in primary forest or secondary growth. They are equally abundant over gravel and mud bottoms but apparently do not occur in water that is continuously turbid.

This species has a limited altitudinal distribution in Borneo and is most abundant below 300 meters (ca. 1000 feet) above sea level, though it has been recorded at 900 meters (Smith, 1931A). In other parts of its range, *chalconota* lives at higher elevations, van Kampen (1923) citing many Javanese localities above 1000 meters and Mertens (1930, 1934) describing it as a montane form in Bali and Sumatra.

Two adults were in the stomach of a young *Natrix maculata.*

Females with enlarged, pigmented ova were collected in all months from April through August. Males were observed calling throughout that period. These two facts plus the collection of larvae during each of those months indicate that the breeding season extends at least from April to September. Information on the remainder of the year is not available.

Geographic variation.—*Rana chalconota raniceps* from Malaya and Borneo differs from *c. chalconota* in the coloration of the upper lip. Though in both forms the lip usually has a whitish stripe, in *raniceps* the light color includes the edge of the lip whereas in *chalconota* the stripe is bordered below by dark pigment. The five Sumatran specimens seen have the coloration of *raniceps.*

The nuptial pad in this species may be constricted along its median edge (see *Secondary sex characters*). All eight males from Malaya have constricted pads, as do 28 out of 43 males from Borneo. None of 23 males from Java and four from Sumatra has constricted pads. The dorsal asperities characteristic of males are more numerous and stronger in males from Borneo and Malaya than in those from Java. Less than one-half of the Javan males have such asperities on the upper eyelids and only two have them on the lores. By contrast, all Malayan and Bornean males examined have the asperities on the eyelids and only one from each area lacks them on the lores. An earlier statement (Inger, 1956) that *labialis* (=*raniceps*) cotypes lack humeral glands is incorrect. Males from all populations have these glands though they are not always well-developed.

The black cephalic markings of the Bornean larvae described above are lacking in 25 larvae from Java. The last also differ from Bornean tadpoles in the papillae of the oral disk. Besides having the short, thick papillae on the posterior lip as described above for Bornean specimens, the tadpoles from Java have a marginal row of distinctly longer papillae.

The populations of *chalconota raniceps* from Sabah, Sarawak, and Kalimantan do not differ from one another in the characters examined.

Range.—*Rana chalconota* occurs from peninsular Thailand to Java, Bali, and Celebes (Mertens, 1930). The subspecies *chalconota raniceps* occurs in Borneo, Malaya, and possibly Sumatra and peninsular Thailand.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Kota Belud District, Kiau, Kina Balu (Smith, 1931A); Sandakan Dis-

trict, Sandakan, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tawau District, Kalaban, Pulo Sebatik. SARAWAK: First Division, Kuching, Matang, Sadong, Santubong (Smith, 1925B), Samunsam valley; Second Division, Gunong Klingkang, Lupar River valley; Third Division, Baleh River near mouth of Putai River, Mengiong River, headwaters of Baleh River; Fourth Division, Akah River, Niah, Pa Brayong, Patah River, Sungei Pesu, Tutoh River. KALIMANTAN: Danau Sriang (van Kampen, 1923), Bandjermasin, Bluu, Kenepai Mountains, Mount Semedum, Sintang.

Rana erythraea (Schlegel)

Hyla erythraea Schlegel, 1837, Abbild. Amph., p. 27, pl. 9, fig. 3—Java.

Rana erythraea Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 65, text fig.; 1920, Rec. Indian Mus., **20**, p. 152; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 222; Smith, 1925, Sarawak Mus. Jour., **3**, p. 33; Inger, 1956, Fieldiana, Zool., **34**, p. 405.

Material examined.—Borneo 504 (3 BM; 488 FMNH; 1 NHMW; 4 NSH; 6 RMNH; 2 USNM); Sumatra 6 (MZB); Great Natuna 1 (BM); Nias 3 (BM); Singapore 2 (FMNH).

Description.—Body slender (males) to moderately robust (females); males 30–45 mm., females 50–75 mm.; head longer than broad; snout pointed, longer than eye, projecting; interorbital subequal to width of eyelid; canthi distinct; lores concave; tympanum distinct, about three-fourths eye diameter.

Tips of fingers dilated into disks having circummarginal grooves; largest disk half of tympanum diameter, less than twice width of phalanges; first finger equal to or longer than second; outer fingers with fringes of skin. Disks of toes smaller than those of fingers; web usually reaching bases of disks on outer edge of first three fingers and on inner edge of fifth; fourth toe with two phalanges free of broad web on outer edge; a low, oval inner and usually a round outer metatarsal tubercle present; tibia 0.50–0.57 of snout-vent.

Skin smooth above; a broad dorsolateral fold; a weak supratympanic fold; ventral surfaces smooth.

Color (in life) usually bright green above and on sides; dorsolateral fold yellow; upper lip and ventral surfaces white; limbs olive above with longitudinal black stripes or rows of dots. In alcohol green areas fade to slate or purplish brown.

Secondary sex characters.—Females are much larger than males. In a large series from Kuching, Sarawak, the snout-vent range of 223 adult females is 48.2–75.0 (mean 65.73 ± 0.34 mm.); the range of 204

adult males is 31.6–44.7 (mean 39.66±0.39 mm.). In the same series, the ratio of tympanum diameter to snout-vent (in terms of thousandths of snout-vent) is larger in males; the ranges are 89–118 (median 104) in males and 73–89 (median 81) in females.

As noted elsewhere (Inger, 1954A), males have nuptial pads on the first fingers and clear asperities on chin and dorsal surfaces. The males also have weak humeral glands.

Larvae.—Body width about half length; eyes dorsal; spiracle lateral, closer to vent than to tip of snout; vent dextral.

Oral disk ventral, subterminal; lower lip and sides of upper lip with papillae; labial teeth I/1–1:I; beaks narrowly edged with black.

Tail convex, end pointed, about twice length of body; length of tail about four times its depth; dorsal fin deeper than ventral one.

Green or brown above, with dark speckling; tail fins mottled; advanced stages with a vertebral and two lateral light stripes. (After van Kampen, 1907; Smith, 1930).

Ecological notes.—In Borneo *erythraea* is found only around the habitations of man, living in artificial ponds, flooded rice fields, and marshes. Its dependence upon man for suitable habitat has restricted its distribution so far to the coast and the immediate neighborhood of the largest rivers. As a result, *erythraea* has not been recorded from elevations above 500 meters.

Forty adults were collected each month for a year at ponds around Kuching. One-third or more of the females of each month's sample contained enlarged eggs. All of the males had well-developed secondary sex characters. Evidently some breeding takes place each month.

Range.—From eastern India and Burma to Sumatra, Java, Celebes, and the Philippine Islands (Boulenger, 1920).

SABAH: Beaufort District, Padas River; Jesselton District, Jesselton; Kinabatangan District, Bukit Kretam; Kota Belud District, Kota Belud; Kudat District, Bongon; Penampang District, Penampang; Ranau District, Ranau. SARAWAK: First Division, Kuching; Fourth Division, Baram River. KALIMANTAN: Bandjermasin, Bengkajang, and Kapuas River (van Kampen, 1923), Pontianak, Sintang.

Rana glandulosa Boulenger

Rana glandulosa Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 73, pl. 8—Sarawak; 1920, Rec. Indian Mus., **20**, p. 181; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 194; Smith, 1925, Jour. Sarawak Mus., **3**, p. 32.

Material examined.—Borneo 150 (5 BM, including; 133 FMNH; 3 NHMW; 5 SM; 3 SNG; 1 USNM); Malaya 3 (BM); Sumatra 1 (ZMA).

Taxonomic notes.—*Rana baramica* is probably the only Bornean ranid that might be confused with *glandulosa*. These two species, which occur together at least in the Baram region of Borneo, are alike in habitus, in general coloration, and in their reduced webbing. Nonetheless, as van Kampen (1923) points out, *glandulosa* has more webbing than *baramica*. In the latter, the web leaves two phalanges of the fifth toe free; in *glandulosa* only one or 1½ phalanges of the fifth toe are free. The fourth toe has three or 3⅓ phalanges free of web in *glandulosa*, 3½ or more in *baramica*. The separation of the outer metatarsals is wider and deeper in *glandulosa* than in *baramica* (fig. 36).

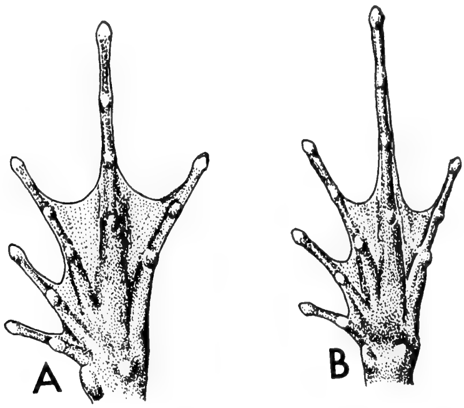


FIG. 36. Ventral view of feet of *Rana glandulosa* (A), and *R. baramica* (B).

Rana glandulosa is the larger of the two, nine females containing enlarged ova measuring 65.0–84.1 mm. whereas seven gravid *baramica* females measure 44.3–66.9 mm. Males differ to the same extent; 13 adults of *glandulosa* measure 58.0–92.9 mm. and nine of *baramica* 38.9–45.6 mm. The relative head width is larger in *glandulosa* and the relative tympanum diameter greater in *baramica* (Table 23). They do not differ in the ratio of tibia to snout-vent.

Description.—Body moderately stout, legs slender but short; adults 65–93 mm.; head obtusely pointed, width 0.32–0.37, length 0.36–0.40 of snout-vent; snout longer than eye, not projecting in profile; nostril much closer to tip of snout than to eye; interorbital usually narrower than upper eyelid; tympanum conspicuous, about ⅔ eye

TABLE 23.—Comparison of body proportions in *Rana glandulosa* and *R. baramica*. Ratios of head width and tympanum diameter are given in terms of thousandths of snout-vent.

	No.	Range	Median	U*	P
		Head width (sexes combined)			
glandulosa	14	320–367	333	21	0.001
baramica	15	301–339	314		
		Tympanum diameter (males)			
glandulosa	7	67–88	72	2	0.001
baramica	7	80–98	94		
		Tympanum diameter (females)			
glandulosa	11	65–81	71	19.5	0.02
baramica	10	70–91	77		

* U of Mann-Whitney test.

diameter; vomerine teeth in oblique groups between posterior halves of choanae, groups usually separated from each other and from choanae by less than length of one group.

Tips of fingers slightly dilated, with interrupted circummarginal grooves; fingers long, first much longer than second; fingers without fringes or flaps of skin; a supernumerary tubercle on all metacarpals. Tips of toes (fig. 36A) like those of fingers, but a little larger; first toe with two phalanges free of web, second with 1½, third with two, fourth with 3 to 3⅓, and fifth with 1 to 1½; an oval inner and a smaller round outer metatarsal tubercle; tibia 0.43–0.49 of snout-vent.

Skin above with low, rounded glands, sides with larger and more prominent glands; no dorsolateral fold; a weak supratympanic fold from eye to axilla; posterior third of venter rugose, remainder smooth.

Color (in alcohol) grayish brown above with small indistinct dark spots; sides spotted; below gray to cream-colored, throat often mottled with dark pigment; limbs with dark crossbars dorsally.

Secondary sex characters.—The sexes do not differ in size. The smallest female containing enlarged ova measures 65.0 mm.; ten females larger than that vary from 66.5 to 84.1 mm. (mean 74.04 ± 2.28). Thirteen adult males (those with vocal sacs) range from 58.0 to 92.9 mm. (mean 73.25 ± 2.21).

Males have paired subgular vocal sacs; the lateral gular skin is wrinkled and thrown into folds superficial to the vocal sacs. A large gland ($7 \times 7 \times 3$ mm. in a 67 mm. frog) is present on the upper arm of all adult males. The nuptial pad is poorly developed; the thin yel-

lowish-gray structure occupies a small oval area dorsomedially near the distal end of the first metacarpal. Minute, translucent asperities are present posteriorly on the back.

Ecological notes.—Twenty-five of the 38 frogs for which detailed habitat notes are available were caught on the ground away from the immediate vicinity of water; 11 were found on the banks of small streams, one "on a tree," and two on swampy ground. Thirty-eight were caught in primary forest, four in secondary growth, and 24 in large clearings. All were captured at night. The reduced webbing suggests that *glandulosa* is not aquatic and its short legs indicate a poor jumper.

Nine-tenths of the Bornean frogs examined were collected within 100 meters of sea level. One frog was taken at 300 meters and another at 600 meters above sea level.

Mature ova (1.5–2.0 mm.) were present in females collected in April, June, and August at Niah, Sarawak. The ova have only a small spot of pigment and may be laid in small, temporary pools separated from streams.

Geographic variation.—None observed.

Range.—Peninsular Thailand (Smith, 1930) and Malaya to Sumatra and Borneo.

Annandale (1917) reported a specimen from Hsipaw (23° N), northern Burma without any descriptive notes. The identification of this frog from a mountainous, subtropical area approximately 1500 kilometers from the next known locality must be confirmed before this remarkable range extension is accepted.

The Palawan specimen recorded by Boulenger (1920) is a *Rana signata*. The specimens from Singapore listed by Boulenger (*ibid.*) are *R. baramica*.

SABAH: Jesselton District, Jesselton, Menggatal; Kudat District, Bongon; Sandakan District, Sandakan, Sepilok Forest Reserve; Sipitang District, Sipitang. SARAWAK: First Division, Kuching (Smith, 1925B); Fourth Division, Baram River, Mount Batu Song, Miri (van Kampen, 1923), Mount Mulu, Niah, Subis, Tangap; Fifth Division, Limbang.

Rana hosei Boulenger. Figure 37.

Rana hosii Boulenger, 1891, Ann. Mag. Nat. Hist., (6), 8, p. 290—Mount Dulit, Sarawak; van Kampen, 1907, Zool. Ergeb. Reise Niederl. Ost-Indien, 4, p.

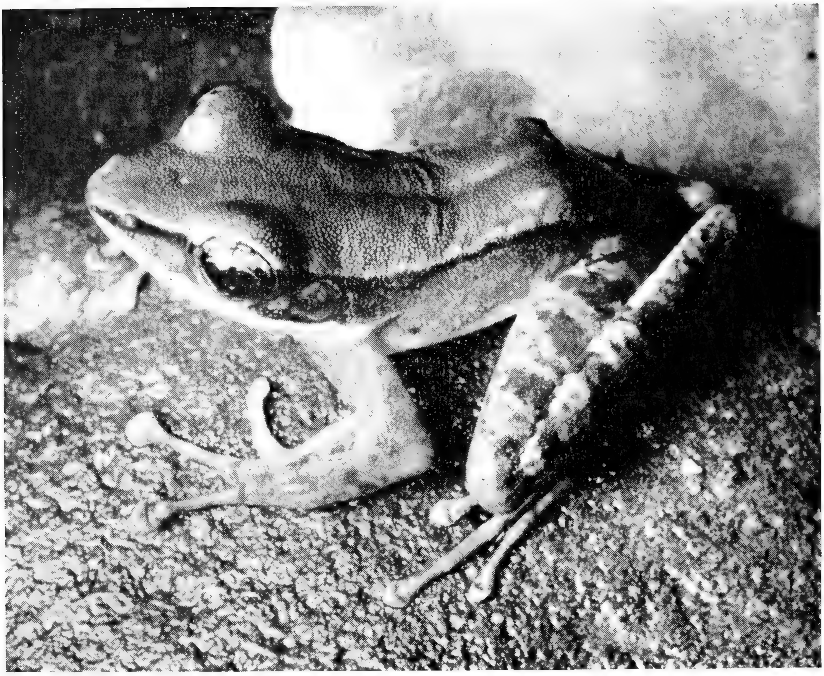


FIG. 37. *Rana hosei*, adult male, 53 mm.

398; 1923, Amph. Indo-Austr. Arch., p. 215, fig. 25; Smith, 1925, Sarawak Mus. Jour., **3**, p. 33; Brongersma, 1937, Zool. Meded., **20**, p. 7.

Material examined.—Borneo 192 (7 BM, including type; 152 FMNH; 9 NSH; 9 RMNH; 15 SM); Malaya 6 (BM); Sumatra 4 (1 SNG; 3 ZMA); Simalur 1 (ZMA); Java 1 (RMNH).

Description.—Body robust; legs long, slender; adult males ca. 50–60 mm., females 85–100 mm.; head triangular, obtusely pointed, width 0.30–0.40, length 0.36–0.40 of snout-vent length; snout projecting, rounded in profile; nostril closer to tip of snout than to eye; eye large, shorter than snout; interorbital narrower than upper eyelid; lores concave, almost vertical; canthi distinct; tympanum conspicuous, two-fifths (females) to three-fourths (males) of eye diameter; vomerine teeth in strong oblique groups beginning between choanae and extending beyond them, groups narrowly separated from each other and from choanae.

Tips of fingers dilated into large disks having circummarginal grooves, outer ones more than twice width of phalanges; disk of third

finger equal to or larger than tympanum in females; first finger equal to or shorter than second; fingers with narrow fringes of skin; supernumerary tubercles on three outer metacarpals. Disks of toes smaller than those of two outer fingers; broad web reaching disks of all toes; outer metatarsals separated to bases; an oval inner but no outer metatarsal tubercle; tibia 0.57–0.66 of snout-vent.

Skin shagreened above; a weak dorsolateral fold; no supratympanic fold; posterior abdominal skin rugose.

Color (in life) dark green above, brownish on sides and on dorsal surfaces of limbs; limbs with black crossbars; upper lips with silvery streak; underside whitish with gray suffusion most pronounced under head.

In alcohol body dark slate gray.

Secondary sex characters.—Females are larger than males. Twelve adult females ranged from 86.0 (the smallest containing enlarged ova) to 98.0 mm. (mean 92.36 ± 0.87 mm.). Males having nuptial pads varied from 42.2 to 66.0 mm. (mean of $30 = 53.83 \pm 0.79$ mm.), though only two were shorter than 49 mm. The tympanum in males is visibly larger than that in females. The ratio of tympanum diameter to snout-vent in 23 Bornean males was 0.069–0.106 (median 0.083) and 0.048–0.059 (median 0.053) in 15 females. The sexes do not differ in other body proportions.

The males have paired subgular vocal sacs that are separated by a thin septum in the mid-line of the throat. The round vocal sac openings are located just inside the corners of the mouth. The gular skin overlying the sacs is not modified. The nuptial pad is a yellowish gray, velvety structure covering the dorsal and median surfaces of the first finger from its base to the level of the subarticular tubercle. The pad extends beyond this point to the base of the disk as a narrow strip on the median edge of the finger. Other asperities, humeral glands, and lineae masculinae are absent.

Larvae.—A small batch of eggs was squeezed from a female (FMNH 136304) and fertilized artificially in a sperm suspension made from the mashed testes of a male (FMNH 136317). Kept in the field laboratory in which the high daily temperature was usually about 32° C, or about 7° higher than surface water in the adjacent river, only two of the eggs developed.

One larva died in stage 24 (Shumway *Rana pipiens* stages) 12 days after fertilization. The operculum is closed on the right side and partly open on the left; oral suckers are absent; the labial tooth rows

have not yet appeared. The second larva, preserved six days later, has not reached the limb bud stage though the operculum is closed and the larval oral apparatus is fully developed.

The failure of most of the eggs to develop casts some doubt on the "normality" of these tadpoles. However, as they have no obvious deformities and as they are the only *hosei* larvae of known parentage, they must stand as representative of larval *hosei*.

Body oval, slightly depressed; no abdominal sucker; eyes dorsal, about two-fifths interorbital width; interorbital one-fourth of body width; mouth terminal; beaks undivided, margins black; lips not expanded into suctorial disk; staggered row of papillae along margin of lower lip and corners of upper lip; labial teeth I:4–4/1–1:III in older larva; gut with a single complete coil in older larva; tail lanceolate, tip rounded; fins subequal, both deep as caudal muscle in posterior half of tail; dorsal fin beginning at end of body.

Total lengths 9.4 and 16.5 mm., tail 0.60–0.66 of total.

Dark gray above, colorless below; caudal muscle dark gray except for light ventral edge; fins colorless.

A metamorphosing frog (FMNH 138694, snout-vent 13.0 mm.) in which the opercular folds are still evident and the tail has just begun to shrink, has diagnostic characters of *hosei:* enlarged digital disks, fully webbed toes, no outer metatarsal tubercle, first finger shorter than second, and supernumerary metacarpal tubercles. The coloration in preservative agrees with that of *hosei*. The angle of the mouth has reached a perpendicular from the front of the eye; no larval oral structures are visible. No sign of a ventral disk is evident. Ranid larvae having ventral, suctorial disks retain the disk until the tail is largely resorbed (see pp. 244 and 257).

Van Kampen (1923) tentatively assigned to *hosei* a series of Javan larvae having a large ventral, suctorial disk. No reason was given for the identification, although Boulenger (1882, p. 89) noted that these particular tadpoles had fully webbed toes and enlarged digital disks. These two characters appear in a number of riparian Malaysian ranids and do not by themselves diagnose any form. The Javan larvae are clearly not conspecific and probably not even congeneric with the Bornean ones just described.

Ecological notes.—*Rana hosei* lives in and along swift, clear streams and large rivers flowing through rain forest or recently logged forests. In Borneo this frog sits on spray moistened rocks, gravel bars, steep banks, or low vegetation, and if disturbed jumps into the swift cur-

rent. Smith (1930) wrote that "the habits of this species are those of a tree frog." Although *hosei* does climb shrubs and small trees on stream banks, it is not arboreal in the sense that it usually is found in vegetation and is relatively independent of water. All but a few of the hundreds collected in Sarawak were on stream banks and about as many on the ground as in vegetation.

The 152 Bornean frogs for which data exist have the following altitudinal distribution: below 300 meters—124; 300–600 meters—8; 600–900 meters—5; 900–1200 meters—15. Van Kampen (1923) reported *hosei* from 1400 meters in Sumatra.

Ova are cream-colored and lack a dark hemisphere indicating a specialized site of oviposition. Ova measure about 2.2 mm. without the gelatinous envelopes.

Geographic variation.—No significant variation observed.

Range.—Malay Peninsula, Sumatra, Simalur, Borneo, and Java.

SABAH: Lahad Datu District, Sungei Pangaruan; Ranau District, Sungei Mamut. SARAWAK: First Division, Bidi, Gunong Poi; Second Division, Lupar River valley; Third Division, Mengiong River, Baleh River near mouth of Putai River, Balingian, Mount Dulit (van Kampen, 1923); Fourth Division, Bario, Long Peluan, Meligong on Akah River, Mount Batu Song, headwaters of Niah River, Pa Jering, Palutan River, Pa Main, Pa Merer, Pa Ra, Pa Ukat, Patah River, Tutoh River. KALIMANTAN: Bluu River, Gunong Seniai, Long Petah, upper Sibau River, Siniai River.

Rana ibanorum Inger. Figure 38.

Rana ibanorum Inger, 1964, Fieldiana, Zool., 44, p. 151—juncture of Baleh and Putai Rivers, Sarawak.

Material examined—Borneo 146+7 series of larvae (FMNH, including type series).

Description.—Body stocky; limbs heavy; snout-vent to about 125 mm.; head slightly longer than broad; snout obtusely pointed; tympanum distinct, half eye diameter; vomerine teeth in oblique groups, narrowly separated from each other and antero-median corners of choanae; lower jaw with a pair of bony projections near symphysis; skin of all dorsal surfaces with a system of short, raised ridges and round tubercles superimposed on a network of radiating, low rugae; small white asperities on dorsal surfaces; a strong supratympanic fold; ventral surfaces smooth.

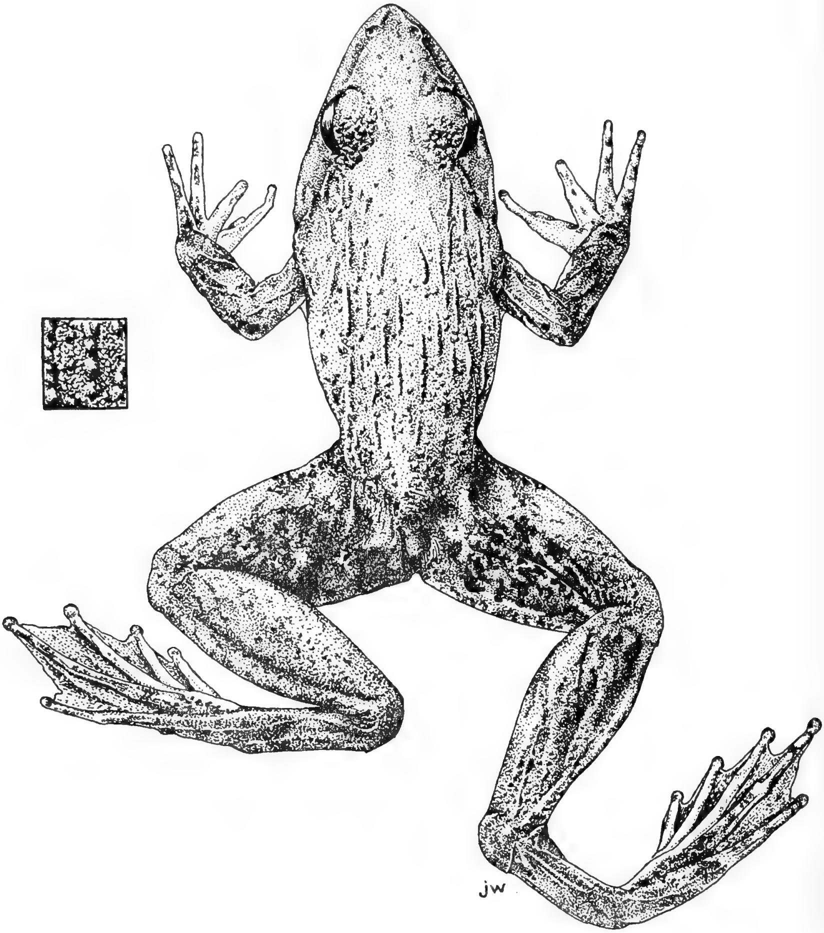


FIG. 38. *Rana ibanorum.* Inset, enlarged view of skin surrounding end of a dorsal ridge.

Fingers with swollen, round tips lacking circummarginal grooves; no supernumerary subarticular tubercles; movable flaps of skin along both edges of second and third fingers and on inner edge of fourth. Toes with tips like those of fingers; all toes broadly webbed to disks; broad flaps of skin along outer and inner edges of foot; subarticular tubercles twice as long as wide; an elongate inner metatarsal tubercle; no outer tubercle; a strong tarsal fold; tibia 0.51–0.55 of snout-vent (median = 0.527; N = 14).

Color (in alcohol) blackish brown above becoming lighter gray on sides; body and top of head with no visible markings; dorsal surfaces

of limbs with obscure dark crossbars; hind face of thigh dark gray with black mottling; lips with narrow light bars; throat whitish with bold dark mottling; rest of ventral surfaces white, immaculate.

Secondary sex characters.—Sex dimorphism in *ibanorum* is identical to that of *blythi* (p. 170). Males lack vocal sacs and nuptial pads. The head of adult males is conspicuously enlarged behind the eyes. At sizes up to about 80 mm. the bony mandibular projection is a knob in both sexes. Beyond that size the projection becomes disproportionately enlarged in males.

Sexual maturity is achieved at about 80 mm. in both sexes. Only one female less than 75 mm. had mature oviducts. Thirteen of 32 in the size class 75–79 mm. and 29 of 44 in the 80–84 mm. class had mature oviducts; only two of 35 in the 85–89 mm. class had immature ones.

Larvae.—Series FMNH 77580, 77582–83, 96003–06; Sarawak Museum unnumbered.

Body oval (fig. 39) width little over half length, slightly depressed; eyes dorsolateral, interorbital equal to internarial distance; eye-nostril distance subequal to nostril-snout and less than internarial; oral disk ventral, subterminal, disk about two-fifths width of head, a little wider than interorbital; upper lip very short, bordered by a continuous row of labial teeth; thick papillae in a single row at lateral corners of upper lip and in a staggered row on lower lip leaving a gap in center of latter; labial teeth I:1–1/1–1:II in all but a few individuals in which lower-most row is represented only by several teeth; lower-most row one-half to two-thirds length of two preceding rows; gap between parts of inner upper row greater than length of each half; labial teeth moderately strong; beaks weakly serrated, black in distal third.

Spiracle sinistral, tubular, on a line connecting eye and root of hind limbs and slightly closer to eye; anus dextral, opening at edge of ventral fin from a tube longer than eye diameter.

Tail strong, tapering rather abruptly to a blunt point, dorsal edge convex, lower edge straight; uniformly deep in proximal half; maximum depth about 0.13 of total length; dorsal fin not as deep as caudal muscle in anterior two-thirds; ventral fin about half depth of dorsal.

Color (in alcohol) usually spotted or mottled with brown above though a few are a uniform dark grayish brown; usually oblique brown streak sloping downward and forward from eye, separated from a brown area below and behind eye; the latter area sometimes divided into two vertical bars; a dark transverse bar across root of

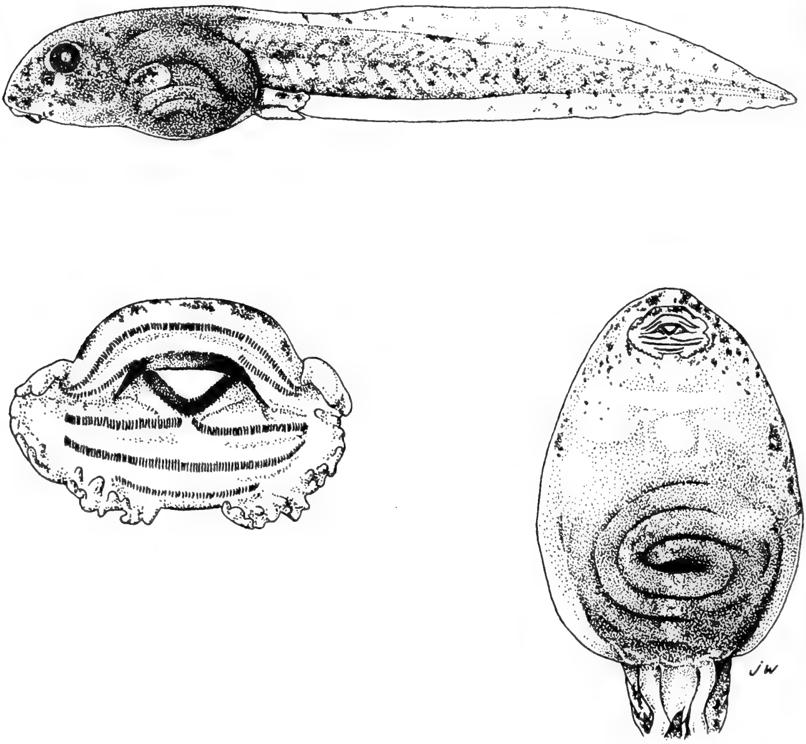


FIG. 39. Tadpole of *Rana ibanorum* from Sarawak.

tail at beginning of dorsal fin; caudal muscle moderately mottled with black, one or two dark bars dorsally; dorsal fins dusted with small clusters of melanophores, no bars or large spots; ventral fin with similar clusters of melanophores is distal half or third only; ventral surface of body usually colorless.

Although the series extends from pre-limb bud stage to the eruption of the fore limbs, the labial tooth count does not vary. Body, total length, and number of tadpoles measured for each stage (Taylor and Kollros, 1946) follow.

Stage	No.	Body (mm.)	Total length
pre-limb bud	4	6.0– 6.7	16.8–18.5
I–V	5	7.5– 8.2	20.1–22.6
VIII–X	2	9.9–10.4	26.4–30.1
XI–XIV	4	9.7–13.4	28.0–30.0
XVI–XVIII	5	11.4–13.9	34.7–37.4
XX	1	10.6	31.4

Two completely metamorphosed juveniles measure 11.9 (FMNH 76953) and 12.7 mm. (FMNH 76944).

The relatively short fourth toe and the fully webbed feet of advanced larvae restrict possible identification to *Rana kuhli* and *Rana ibanorum*. Only adults of the latter have a flap of skin along the inner margin of the fourth finger and elongate subarticular tubercles under the toes; both characters are found in advanced larvae collected in the same stream inhabited by adult *ibanorum*.

These larvae differ from those of *kuhli* (fig. 40) in many ways, most conspicuously in the absence of distinct barring on the dorsal fin. Ventrally *ibanorum* larvae are colorless whereas those of *kuhli* have a dark network giving their undersides a greyish cast. The single, though staggered, row of posterior papillae also distinguished *ibanorum* from *kuhli*, which has two distinct rows of papillae.

The gap between parts of the inner upper tooth row is greater in *ibanorum* (at least equalling length of each half) than in *kuhli* (usually less than length of each half), whereas the posterior-most tooth row is relatively longer in *ibanorum* (usually more than one-half length of preceding row; usually less than one-half in *kuhli*).

Larval *blythi* differ from *ibanorum* in the dental formula (I/1–1 : II in the former, I:1–1/1–1: II in the latter).

Ecological notes.—This species is abundant along streams (ca. 10–30 m. wide) in hilly forested country. The type locality is a recently cut-over area, but most specimens seen subsequent to that collection were caught in primary or partly logged rain forest. Frogs have been caught on clay or rocky banks. No specimens have been collected more than 10 m. from the water's edge.

Larvae were caught in small pools at the edge of streams and in a few cases in pools completely cut off from the current by temporarily lowered water level. All of these pools had sand or gravel bottoms covered with accumulations of dead leaves and a thin layer of silt.

Most (123) of the specimens were collected between 50 and 300 meters above sea level; 20 were caught at 300–600 m. and three at 750–900 m. Apparently *ibanorum* does not occur in flat alluvial areas such as around Niah, Sarawak, or in the lower Rejang basin.

Range.—Sarawak and Kalimantan.

SARAWAK: Second Division, Lupar River valley; Third Division, Baleh River near mouth of Putai River, Mengiong River, headwaters of Baleh River; Fourth Division, Lapu Wei and Pa Mercer (Kelabit

Plateau), Long Peluan, Melana River, Meligong, Sungei Pesu, headwaters of Tutoh River. KALIMANTAN: Long Petah.

Rana kuhli Duméril and Bibron

Rana kuhlii Duméril and Bibron, 1841, Erp. Gén., **8**, p. 384—Java; Boulenger, 1920, Rec. Indian Mus., **20**, p. 62; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 178; Smith, 1925, Sarawak Mus. Jour., **3**, p. 9; *ibid.*, **3**, p. 32; Inger, 1956, Fieldiana, Zool., **34**, p. 403.

Material examined.—Borneo 184 (9 BM; 111+2 lots of larvae FMNH; 1 NSH; 23 RMNH; 27 SM; 2 SNG; 2 UMMZ; 9 USNM); China 6 (FMNH); Thailand 4 (FMNH).

Taxonomic notes.—Despite its wide range, *kuhli* has not undergone enough local differentiation to warrant recognition of subspecies.

Description.—Body stocky, limbs heavy, relatively short; snout-vent to about 75 mm.; head as broad as long; snout broad, obtusely pointed; tympanic annulus usually not visible through skin, though present; vomerine teeth in closely set, oblique groups, between and behind choanae; lower jaw with a pair of toothlike projections near symphysis; skin of back rugose, with low ridges radiating from low, rounded warts; dorsal surface of hind limb with warts (see *Geographic variation*); a strong temporal fold; no dorsolateral fold.

Fingers bluntly rounded; first finger longer than second; no supernumerary metacarpal tubercles; distinct flaps of skin along both edges of second and third fingers; tips of toes distinctly expanded into round disks lacking grooves; web reaching disks of all toes as a broad sheet; a flap of skin on outer edge of fifth toe and on inner edge of first toe; subarticular tubercles oval but not elongate; inner metatarsal tubercle oval, shorter than first toe; no outer metatarsal tubercle; tarsus with a thick ridge extending proximally from metatarsal tubercle.

Color (in life) pale brown above with or without darker spots; a dark, oblique temporal stripe of varying width usually present; lips usually barred with blackish brown; limbs with dark crossbars dorsally; throat usually white mottled with gray; abdomen immaculate white or cream-colored.

Secondary sex characters.—The relative enlargement of the head and mandibular processes of male *kuhli* are well known (Boulenger, 1920; Pope, 1931). Males apparently reach a greater snout-vent length, the range in 13 Bornean males having nuptial pads being 43.9–74.3 mm. Fifteen Bornean females contained mature ova; they measured 50.7–67.4 mm. As Pope has shown, the greater size

achieved by males is accounted for by the progressive enlargement of the head. Subtracting the head length from snout-vent gives a range of 26.2–39.4 mm. for the above males and 30.5–40.8 mm. for the females.

Boulenger stated that males lack nuptial pads, but Pope said that Chinese specimens had them on the first finger. In Bornean males the normal site of the nuptial pad is sharply set off from the remainder of the skin on the first finger by a distinct yellowish or brownish tinge. But the dense cluster of minute spines composing the usual ranid nuptial pad are absent.

Males do not have vocal sacs.

Larvae.—Twenty-seven tadpoles (fig. 40) in various stages of hind limb development form the basis of the following description.

Body oval, width about two-thirds length, slightly depressed; eyes and nostrils dorsal; interorbital and internarial spaces subequal, equal

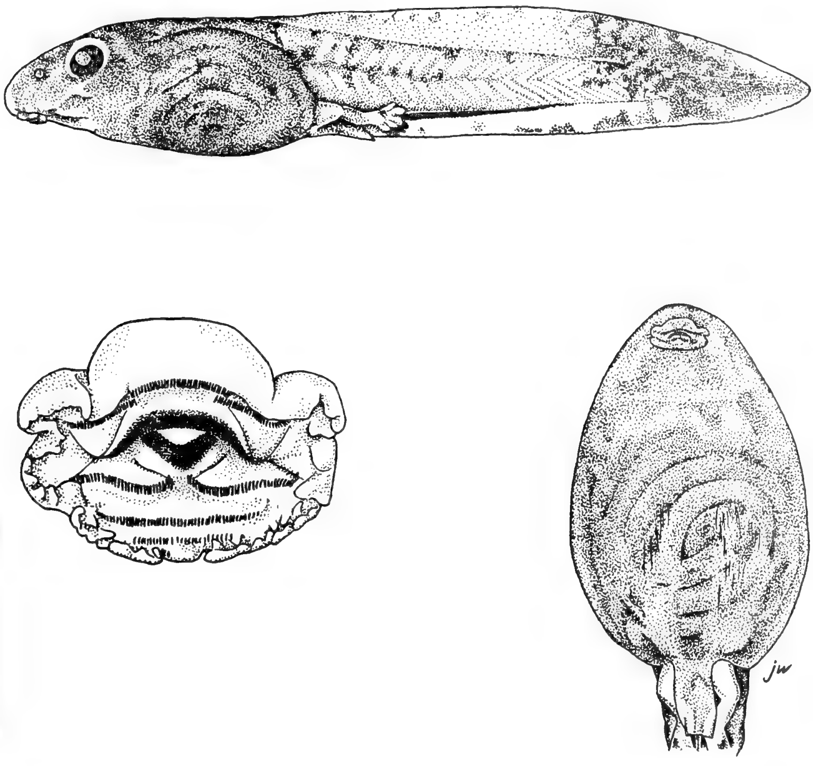


FIG. 40. Tadpole of *Rana kuhli* from Sarawak.

to nostril-snout distance but longer than eye-nostril; oral disk ventral, subterminal, disk about one-third head width, equal to interorbital; upper lip short, bordered by row of teeth; thick, short papillae in a single row at lateral quarters of upper lip and in two rows across lower lip; no gap in papillae of lower lip; labial teeth I:1+1/1+1:II (25 specimens); halves of inner upper tooth row separated by distance equal to or less than length of each half; inner lower row with very narrow gap in center; two inner lower rows subequal, outer-most row one-third to one-half length of inner ones; labial teeth strong; beaks weakly serrated, black in distal third.

Spiracle sinistral, tubular, just below line connecting eye and root of hind limb, closer to eye; anus dextral, opening at end of tube at margin of ventral fin, tube longer than eye.

Tail strong; tapering gradually in last quarter to obtuse point; dorsal edge convex, ventral edge straight, maximum depth at center about 0.20 of total length; dorsal fin deeper than caudal muscle in distal half; ventral fin about two-thirds depth of dorsal.

Color (in alcohol) dark gray above, lighter gray below formed by a dark network; head without definite pattern; an obscure dark transverse bar at origin of dorsal fin; caudal muscle with dark spots extending upward to form large spots or bars on dorsal fin, especially in distal half; ventral fin with widely spaced black spots in proximal half, densely spotted distally.

Larvae in pre-limb bud stages have total lengths of 20.0–20.6 mm., of which the tails constitute 0.59 to 0.63 per cent. The oldest larvae (Stage XVIII), in which the labial teeth are eroded even though the fore limbs have not erupted, measure 35.4–38.4 mm. with the tails forming 0.62–0.65 per cent. The youngest larvae already have the full complement of labial teeth.

The fully webbed toes, relatively short fourth toe, and oval but not elongate subarticular tubercles of advanced larvae confirm the association with adult *kuhli*.

The Bornean larvae agree with the description of *kuhli* tadpoles from northern Thailand (Smith, 1917) and southern China (Pope, 1931), except that the tail is apparently more heavily spotted and the nostrils somewhat farther apart in Bornean specimens.

Differences between tadpoles of *kuhli* and the closely related *ibanorum* are noted under the latter (p. 195).

Ecological notes.—In Borneo *kuhli* is most abundant along small, clear streams flowing with moderate speed through primary rain for-

est. Sixty-one of 84 for which detailed information is available come from such situations. At Deramakot, Sabah, no specimens were caught along the muddy, almost stagnant streams in the swamp forest, whereas nine were collected along the rocky banks of a clear stream draining one of the ridges. At Kalabakan, Sabah, only six were caught in primary forest and 12 around rain puddles in the roads through a logged area. At Matang, Sarawak, *kuhli* was one of the commonest ranids along the rocky, swift Sungei China. Only two specimens were caught in the city of Sandakan along drainage ditches.

The last two are the only Bornean *kuhli* to come from a habitat similar to the one this species occupies in Fukien, China (Pope, 1931). The typical habitat in Borneo is the same as the one attributed to *kuhli* in Sumatra and Java (Mertens, 1934).

The altitudinal range of *kuhli* seems to be more extensive in Borneo than elsewhere. All the material I collected comes from within 300 meters of sea level. Ten specimens in the Sarawak Museum were obtained at 1900 meters on Mount Murud and other Bornean specimens have been recorded from 600–1295 meters (Smith, 1925B, 1931A). Mertens considered *kuhli* to be a distinctively montane form in Sumatra and Java, and Smith (1917) found it most commonly at elevations above 700 meters in Thailand.

Pope (1931) suggested that *kuhli* avoided swift, shaded streams in Fukien because its body form was poorly adapted to withstand the force of the water. The references of Smith and Mertens and my own observations demonstrate that *kuhli* not only can get along in such situations, but actually seems very well adapted to them. By remaining behind large boulders, the specific situation in which it is usually found in Borneo, *kuhli* is able to avoid the force of the current.

Copulation in such a place poses no problem to any aquatic frog, although larvae were found only in a semi-isolated pool immediately adjacent to a swift stream.

Females with enlarged ova were collected May–August. Larvae were caught in August.

Geographic variation.—Frogs from five widely separated localities in eastern Sabah have much wartier skin, especially on the hind legs (fig. 41), than do those from Sarawak (from three widely separated areas). In the former sample, the tibia has numerous large and small round warts each tipped with a large whitish cone surrounded by clusters of much smaller, whitish asperities. These asperities cover most of the surface of the tibia. In Sarawak frogs the warts of the

tibia are very low, less dense than in the other sample, and usually bear only a central whitish asperity. The frogs seen from Kalimantan were not well preserved, but they seem to have skin like the Sarawak frogs.

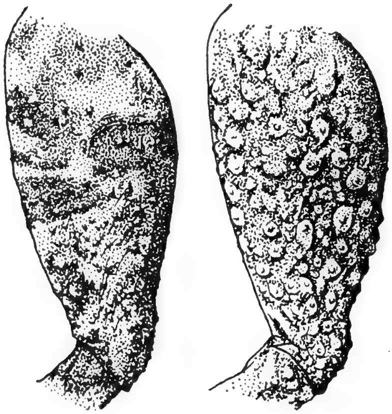


FIG. 41. Skin of lower leg of *Rana kuhli* from Sarawak (left) and Sabah (right).

An oblique, black stripe from the eye across the tympanic region to the arm insertion is a common feature in *kuhli*. The stripe is narrower and less frequently observed in frogs from eastern Sabah than in those from other parts of the island. In Table 24 "Wide" indicates

TABLE 24.—Frequency and width of temporal stripe in *Rana kuhli*.

	Wide[1]	Thin[1]	Absent
Kalimantan	11	3	1
Sarawak	20	3	0
Western Sabah	6	2	0
Eastern Sabah	2	16	9
China: Fukien	2	4	0
Thailand	3	1	0

[1] See text for explanation.

that the stripe covers half or more of the space between the supratympanic fold and the rictus and "Thin" less than half that space.

In general, Sarawak frogs are more heavily pigmented. The Sabah frogs lacking a temporal stripe usually also lack dark spots on the back, whereas the others have small round black spots on the dorsum. The Sarawak frogs have larger and usually confluent spots dorsally. Referring to a pattern of large confluent spots as "heavy," 19 of the Sarawak frogs have heavy dorsal pigment and seven light. None of the Sabah frogs have "heavy" patterns. A blackish stripe

runs along the anterior face of the upper arm in 82 per cent of the Sarawak samples, but appears in only one-sixth of those from eastern Sabah. The other Bornean samples are too poorly preserved for accurate observation.

The Fukien and Thailand specimens seen have dark markings forming a broad W across the back anteriorly and usually a few small, isolated spots posteriorly. A dark stripe is present on the upper arm in four of the six from Fukien and in three of the four from Thailand.

The relative size of the space between the nostrils is greater in the Sarawak frogs than in those from other parts of Borneo (Table 25).

TABLE 25.—Ratio of internarial width to snout-vent length in *Rana kuhli* from various parts of Borneo.

	No.	Range	Median
Sarawak	17	0.077–0.092	0.084
Sabah			
western	7	0.063–0.083	0.072
eastern	18	0.065–0.083	0.073
Kalimantan	5	0.068–0.079	0.072

The Kruskal-Wallis analysis of variance (Siegel, 1956) applied to these ratios shows the inter-sample differences to be statistically significant ($H = 25.61$; $P < 0.001$). This ratio in the six Chinese *kuhli* at hand has a range of 0.067–0.086 (median 0.076); using the Mann-Whitney U test, this sample probably differs from the Sarawak one at the 0.05 level ($U = 20.5$) but not from the others. The difference between the Sarawak and other Bornean samples is not related to overall differences in head width. Since the narrower the internarial space the more dorsal the position of the nostrils, *kuhli* from Sarawak have this aquatic adaptation less well developed than do the other Bornean samples.

The six Chinese and one Thai male have nuptial pads on the first and second fingers. Males from Sabah and Sarawak have such pads only on the first finger. The difference between continental and Bornean males is not accounted for by seasonal differences as most of the Sarawak females collected with the males have mature ova.

Range.—From southern China southwards through the Malay Peninsula to Java, Sumatra, Borneo, and Celebes (van Kampen, 1923).

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Kota Belud District, Kenokok (Smith, 1931A), Kiau, Kappa (van Kampen, 1923), Kalawat (*ibid.*); Ranau District, Bundu Tuhan, Ranau, Sungei Kepungit, Tenompok (Smith, 1931A); Sandakan District, Sandakan, Sapagaya Forest Reserve; Tawau District, Kalabakan. SARAWAK: First Division, Kuching, Gunong Ngili, Gunong Temiang, Matang, Mount Penrissen, Samunsam valley; Second Division, Lupar River valley; Third Division, Baleh River near mouth of Putai River, Mengiong River, headwaters of Baleh River, Mount Dulit (Smith, 1925B); Fourth Division, Baram River, Pa Main; Fifth Division, Mount Murud, Pa Brayong. KALIMANTAN: Bluu, Kenepai Mountains, Liang Kubung, Nanga Raun, Mount Semedum.

Rana laticeps Boulenger. Figure 42.

Rana laticeps Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 20, pl. 1, fig. 1—Khasi Hills, Assam; Smith, 1925, Sarawak Mus. Jour., **3**, p. 32.

Material examined.—Borneo 19 (13 FMNH; 6 SM); Assam 5 (BM, types).

FIG. 42. *Rana laticeps*, 40 mm.

Taxonomic notes.—This species is very similar to *Rana kuhli* from which it differs only in size and extent of webbing. In those two characters, however, the differences are striking. The four gravid females of *laticeps* seen range from 32.0 to 39.5 mm., whereas the size range of gravid females of *kuhli* from Borneo is 50.7–67.4 mm. None of the toes of *laticeps* is broadly webbed to the disk; in *kuhli* usually all

of the toes are broadly webbed to the disks. Movable flaps of skin are present on the outer edge of the fifth toe and along both edges of the second and third fingers of *kuhli*; *laticeps* never has movable flaps in those positions though it usually has a fixed ridge of skin along the fifth toe.

These two species have overlapping ecological ranges in Sarawak. *Rana laticeps* occurs in wet seepage areas and small intermittent streams (see below); it was not observed in small permanent streams, which are the principal habitat of *kuhli*. A few young individuals of *kuhli* were caught in an intermittent stream simultaneously with *laticeps*.

Description.—A small species of *Rana,* snout-vent of Bornean adults to 40 mm.; body moderately stocky; limbs thick; snout obtusely pointed or rounded; tympanum present, not visible through skin; vomerine teeth in closely set, oblique groups, between and behind choanae; lower jaw with a pair of bony prominences near symphysis; skin of back rugose, the wrinkles or ridges running in all directions, those at rear of body radiating from low, conical warts; a strong temporal fold; no dorsolateral fold.

Tips of fingers slightly swollen; first finger longer than second; no supernumerary metacarpal tubercles; edges of second and third fingers of some species with narrow ridges of skin; fingers never with freely movable flaps of skin; tips of toes swollen into distinct, small disks; broad web not reaching disks of any toes; fourth toe with three phalanges free of broad webbing which continues to disk as a narrow fringe; inner edge of third toe with two phalanges free of broad web; a ridge but no freely movable flap of skin along outer edge of fifth toe; an oval, inner metatarsal tubercle, much less than length of first toe; no outer metatarsal tubercle; a weak tarsal ridge; tibia 0.48–0.52 of snout-vent (median 0.494; N = 5).

Color (in life) dark brown above with black spots; a dark red or black interorbital bar; red and black bars on side of head; throat gray or white with brown spots; chest, belly, and ventral surfaces of legs lemon yellow. In preservative the yellow fades to white and the red bars on the head fade to pale brown.

Ecological notes.—*Rana laticeps* has been found in Borneo only in virgin or partly logged rain forest. Most of the frogs for which I have data were caught in aquatic situations. Five were collected in a small stream, consisting of pools (up to ca. 30 cm. in diameter and to 4 cm. deep) between rocks and having only a trickle of water except immediately after rains. The silty bottom of the pools was strewn with

dead leaves and gravel. Five others were caught in a clayey seepage area at the head of a small stream. The leaf litter was about 2 cm. deep. One specimen was found in an isolated pool at the top of a hill. Two were collected away from water, one on dead leaves and one under a log.

By day this species usually hides under leaves or other debris of the floor. Of 10 specimens caught during the day, nine were found under leaves, logs, or rocks; the tenth was sitting on a leaf. Three collected at night were sitting in the open at the edge of a small stream.

Smith (1925B) recorded six specimens from 915 meters in Sarawak. The 13 specimens collected by our field party were obtained between 100 and 300 meters above sea level. In Malaya *laticeps* is known from elevations between 900 and 1200 meters (Smith, 1922). The type locality is in the Khasi Hills, Assam, which rise to about 2000 meters above sea level.

The three gravid females for which data are available were collected September, October, and November.

Geographic variation.—Bornean representatives of this species have narrower heads and shorter legs than do frogs from the continent (Table 26). Differences in snout-vent length do not account for differences in body proportions. Females from the two areas are approximately equivalent in size yet differ in body proportions in the same way as the males.

TABLE 26.—Geographic variation in *Rana laticeps*. Data on mainland specimens from Boulenger (1920).

	Snout-vent (mm.)	Head width[1]	Tibia[1]	No.
		Males		
Mainland	29–51	467–482 (474)	510–552 (525)	3
Borneo	25.9–29.2	380–389 (384)	482–494 (488)	2
		Females		
Mainland	34–41	415–442 (426)	514–571 (547)	5
Borneo	32.0–39.5	375–400 (391)	481–515 (498)	3

[1] Head width and tibia length in terms of thousandths of snout-vent. Medians in parentheses.

Though they are smaller than males from the continent, the two Bornean males have distinctly enlarged mandibular odontoids suggesting that they are reproductively mature.

Range.—Assam to Borneo.

SARAWAK: First Division, Mount Gadin (Smith, 1925B), Mount Penrissen; Third Division, Mengiong River; Fourth Division, Sungei Pesu.

Rana limnocharis limnocharis Boie

Rana limnocharis Boie *in* Wiegmann, 1835, Nova Acta Acad. Leop. Carol., **17**, p. 255—Java; Boulenger, 1920, Rec. Indian Mus., **20**, p. 28 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 167, fig. 23; Smith, 1925, Sarawak Mus. Jour., **3**, p. 32.

Material examined.—Borneo 66 (10 FMNH; 13 MCZ; 1 MZB; 27 RMNH; 15 SM); Sumatra 11 (3 FMNH; 8 MZB); Singapore 5 (FMNH).

Description.—Body moderately stocky; limbs short, moderately heavy; adult males 32–50 mm., females 48–58 mm.; head longer than broad; snout rounded; tympanum visible, about three-fifths eye diameter; irregular skin folds on back; a supratympanic fold from eye to axilla.

Finger tips not expanded; first finger longer than second; fingers without fringes of skin. Toes pointed, tips not expanded; web deeply excised, leaving at least one phalanx of each toe free; fifth toe with 1⅓–2 and fourth with three phalanges free; a ridge or narrow flap of skin usually present on outer edge of fifth toe; a raised, oval inner and a low, round, outer metatarsal tubercle.

Color (in alcohol) grayish or brownish above with large black markings, often in form of scapular W; many with light vertebral band or line; limbs with dark crossbars; underside whitish, immaculate except in males.

Secondary sex characters.—Bornean males having nuptial pads vary from 32.2 to 48.6 mm. (mean of 23 $= 42.18 \pm 0.85$). The smallest Bornean female seen containing pigmented ova measures 48.7 mm. and the largest 58.0; the mean of 15 is 52.99 ± 0.78 mm.

As in the Philippine form, *l. vittigera* (Inger, 1954A), the males have median subgular vocal sacs, black M-shaped bands across the throat, nuptial pads on the first fingers, and colorless ventral asperities.

Larvae.—Body oval, width about two-thirds length; eyes dorsal; spiracle sinistral, lateral, about equidistant between base of tail and tip of snout; vent dextral.

Mouth ventral, subterminal; a single row of papillae laterally on upper lip, a single or double row on lower lip; papillae of lower lip

with a wide median gap; labial teeth I:1–1/III, outermost row of lower series about half length of second row; beaks edged with black.

Tail less than twice length of body; dorsal margin convex, ventral straight; tip attenuated, length about four times the depth; fin deeper than muscle.

Color (in alcohol) of head and body dark gray; fins faintly mottled; dorsal part of caudal muscle with a row of dark spots.

The description is based on larvae (FMNH 101004) from Singapore.

Ecological notes.—*Rana limnocharis,* like *cancrivora,* is found in Borneo only where man has long been in residence and has destroyed the original vegetation. It is found, therefore, only in the lowlands along the coasts and in the lower reaches of the larger rivers.

Geographic variation.—Differences between the Bornean population and *limnocharis vittigera* of the Philippine Island have already been pointed out (*ibid.*). The Bornean frogs agree with those of Singapore, Sumatra, and Java in having outer metatarsal tubercles and a ridge or flap of skin on the fifth metatarsal—two of the characters distinguishing *l. limnocharis* from *l. vittigera.*

Range.—Southern and eastern Asia, Sumatra, Borneo, Java, and the Lesser Sundas as far eastward as Flores (Boulenger, 1920).

Although van Kampen (1923) lists "North Borneo" in the range of *limnocharis,* I have found no specimen in any collection from that part of the island.

SARAWAK: First Division, Gadin and Matang (Smith, 1925A), Kuching, Gunong Ngili, Sadong, Santubong, Gunong Temiang; Second Division, Saratok (*ibid.*), Lupar River valley. KALIMANTAN: Bengkajang and Mandor (van Kampen, *op. cit.*), Mekor, Melawi River, Nanga Raun, Singkawang, Sintang.

Rana luctuosa (Peters)

Limnodytes luctuosus Peters, 1871, Monatsber. Akad. Wiss. Berlin, **1871**, p. 579—Sarawak; 1872, Ann. Mus. Civ. Genova, **3**, p. 43, pl. 6, fig. 1.

Rana luctuosa Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 68; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 196; Smith, 1931, Bull. Raffles Mus., no. 5, p. 16; Inger, 1954, Jour. Washington Acad. Sci., **44**, p. 250.

Rana decorata Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat., (3), **2**, p. 145, pl. 10, fig. 1—Kina Balu, Sabah.

Material examined.—Borneo 30 (6 BM; 1 FMNH; 1 MCG, type; 2 NMB; 18+series of larvae SNM; 2 SM); Malaya 6 (5 BM; 1 SNM).

Description.—Habitus moderately stocky; head longer than broad, width about one-third of snout-vent; snout rounded at tip, longer than eye, projecting slightly; nostril above symphysis, closer to tip of snout than to eye; interorbital wider than upper eyelid; tympanum conspicuous, three-fourths eye diameter or larger; vomerine teeth in oblique groups between choanae, groups separated from each other and from choanae by length of one group.

Finger tips only slightly dilated, all with horizontal circummarginal grooves, disks less than half width of tympanum; first finger longer than second; second and third fingers usually with narrow fringes of skin; no supernumerary metacarpal tubercles. Tips of toes subequal to finger tips, with circummarginal grooves; first and and fifth with two phalanges free of broad webbing; web usually to disks as a narrow fringe; outer metatarsals separated by groove in distal two-thirds, by web in distal fifth; a weak, oval inner metatarsal tubercle; a weak, round outer metatarsal tubercle present in approximately one-half of sample; tibia 0.51–0.54 of snout-vent; adult males 53.0–58.8 mm.

Skin smooth; no dorsolateral fold; a band of dermal glands from eye to groin occupying lateral third of back and upper half of side; no tympanic fold; no rictal glands; ventrum rugose posteriorly, otherwise smooth.

Color (in alcohol) light chocolate brown on back and top of head; a thin light dorsolateral line from tip of snout along canthus and edge of upper eyelid to groin; sides of head and body dark brown; ventrally head and chest blackish brown, abdomen lighter; limbs brown above with broad cream-colored bars or vermiculation.

Secondary sex characters.—Adult males (over 53 mm.) have humeral glands, approximately 4 mm. long in a 56 mm. male. Vocal sacs, nuptial pads, and lineae masculinae are absent.

Larvae.—Body subspherical; spiracle closer to eye than to root of tail; oral disk subterminal; lower lip with single continuous row of short papillae; three to five markedly larger papillae laterally; dental formula I:4–4/1–1:III in all three examined.

Stage XVIII larva 27.0 mm., head and body; tail 49.0 mm.

Five frogs with vestiges of the tail measure 29.4–32.2 mm., snout-vent; the typical adult color pattern is present in all.

Ecological notes.—Flower (1896) found *luctuosa* adults in grass around small ponds and larvae in the same ponds on Penang Island. No other habitat information is available. This species is probably

not aquatic except during the breeding period; the reduced webbing is typical of semi-terrestrial frogs. In Borneo *luctuosa* has been collected between 400 and 1200 meters above sea level. In Malaya it has been caught at elevations between 600 and 1200 meters.

Geographic variation.—Although the dorsal pattern is the same in Malayan and Bornean samples, frogs from Malaya lack the bold, cream-colored bars found on the ventral surfaces of the limbs of Bornean specimens.

Bornean frogs are larger than Malayan ones. Three adult (judging by the presence of humeral glands) males from Malaya measure 42.7–44.5 mm.; Flower gave the size range of Penang Island specimens as 45–50 mm. Fifteen Bornean males vary from 53.0 to 58.8 mm.; the metamorphosing frogs (see above) are the only others in this sample.

Range.—This species is known from the northern half of Malaya, Sarawak, and western Sabah.

SABAH: Kota Belud District, Kiau and Kaung, Kina Balu. SARAWAK: First Division, Kuching, Matang; Fourth Division, Akah River, Bario.

Rana macrodon Duméril and Bibron

Rana macrodon Duméril and Bibron, 1841, Erp. Gén., **8**, p. 382—Java; Blanford, 1881, Proc. Zool. Soc. London, **1881**, p. 225, pl. 21, fig. 4; Flower, 1896, Proc. Zool. Soc. London, **1896**, p. 898 (part); Boulenger, 1920, Rec. Indian Mus., **20**, p. 40 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 174 (part); Smith, 1930, Bull. Raffles Mus., no. 3, p. 98 (part).

Rana macrodon macrodon Inger, 1954, Fieldiana, Zool., **33**, p. 275; 1956, *ibid.*, **34**, p. 402.

Material examined.—Borneo 307 (5 BM; 288 FMNH; 2 NHMW; 1 SNM; 1 RMNH; 10 SM); Malaya 12 (6 BM; 1 FMNH; 2 JRH; 3 SNM); Riouw Archipelago 1 (SNM); Siberut Island 7 (SNM); Java 7 (2 BM; 5 RMNH); Sumatra 5 (2 NMB; 3 SNG).

Description.—Body stocky; limbs heavy, moderately long (tibia 0.45–0.56 of snout-vent); snout-vent to well over 125 mm.; head (fig. 32B) slightly longer than broad (Table 21); snout obtusely pointed; canthus rostralis obtuse, poorly defined; lores very oblique, slightly concave; tympanum always visible; vomerine teeth in two large, oblique groups beginning near anteromedian corners of choanae, the groups narrowly separated; lower jaw with a pair of bony projections near symphysis; skin of back smooth in adults, frogs under 75 mm. with inverted V-shaped ridge between shoulders and scattered round tubercles; a strong temporal fold; no dorsolateral fold.

Fingers bluntly rounded; first longer than second; no supernumerary metacarpal tubercles; distinct ridges (not flaps) of skin along inner edges of second and third fingers; tips of toes expanded into round disks lacking grooves; web reaching disks of all toes as a broad sheet, membrane excised to base of middle subarticular tubercle of fourth toe between fourth and fifth toes (Table 22); movable flaps of skin on outer edge of fifth toe and on inner edge of first; subarticular tubercles oval; inner metatarsal tubercle oval, shorter than first toe; no outer metatarsal tubercle.

Color (in life) light chocolate brown to red, usually with small obscure dark spots on back; a straight interorbital black bar; lips usually with broad black bars; no black tympanic stripe running back from eye, though a small dark spot may be present on tympanum; limbs with dark crossbars or mottling; underside pale creamy white, throat usually spotted with black, less often chest spotted; underside of web usually black. In alcohol, dorsal color dark brown. About one-sixth of specimens have a light mid-dorsal line or band.

Secondary sex characters.—Sex dimorphism in *macrodon* is identical to that in *blythi* (p. 170): males lack vocal sacs and nuptial pads; the heads of adult males are larger than those of females. The ratio of head length to snout-vent in adult Bornean males varies from 0.415 to 0.488 (median 0.436; N = 14) and in females from 0.383 to 0.425 (median 0.401; N = 13). Head-width ratios are given in Table 21. The differences between the sexes in both ratios are statistically significant at the 0.001 level (using the Mann-Whitney U test). The bony projection of the mandible is conspicuously longer in males than in females.

Sexual maturity is reached at about 70–75 mm. Five of eight females in the 70–74 mm. class had mature oviducts (enlarged and convoluted); only two of nine in the 65–69 mm. class had mature oviducts; only two of 26 in the 75–79 mm. class had immature oviducts. Four of the Bornean females examined are longer than 120 mm., the largest being 126.9 mm. Five Bornean males exceed 120 mm., the maximum being 128.0 mm.

Larvae.—Flower (1899) ascribed tadpoles collected on Penang Island to "*macrodon*," which he considered to consist of the two forms called *blythi* and *macrodon* in this paper. Although *R. blythi* occurs on Penang Island, Flower's larvae cannot be assigned to that species with certainty for two reasons. First, because Flower did not describe characters of advanced larvae, the adults to which his specimens belong cannot be determined. Secondly, his tadpoles differ from those definitely associated with *blythi* (see p. 171).

TABLE 27.—Geographic variation in body proportions of adult *Rana macrodon*. Values of proportions given in terms of thousandths of snout-vent length. Kruskal-Wallis analysis of variance (Siegel, 1956) applied.

	Males			Females		
	No.	Range	Median	No.	Range	Median
			Tibia/snout-vent			
Borneo	17	490–562	527	14	453–561	515
Malaya	6	417–495	459	3	450–460	459
Siberut	4	477–516	492	1		495
Java	5	432–513	496	2	474–483	479
	H=19.04	P= <0.001				
			Head length/snout-vent			
Borneo	14	415–488	436	13	383–425	401
Malaya	5	425–465	456	2	378–409	393
Siberut	4	439–455	448	1		390
	H=6.169	P=0.047				
			Head width at tympanum/snout-vent			
Borneo	14	376–444	398	16	344–416	375
Malaya	9	387–467	452	3	336–441	400
Siberut	4	369–389	383	1		345
Java	4	386–429	393	2	348–375	361
	H=18.85	P= <0.001				
			Head width before eyes/snout-vent			
Borneo	14	241–274	254	16	229–276	246
Malaya	9	244–299	282	3	230–268	266
Siberut	4	247–256	250	1		245
Java	4	255–274	261	2	237–259	243
	H=14.336	P=0.004				

Schijfsma (1932) recorded larvae from Java but gave no justification for the identification other than general similarity to Flower's description. She noted, however, that the Javan larvae had only a single row of teeth on the upper lip (I:1–1 in Flower's specimens) and a less acutely pointed tail than Flower's larvae. Thus Schijfsma's larvae differ from the Penang specimens in the same ways as Bornean larvae of *blythi* (p. 173). The last differ from Schijfsma's in having the spiracle midway between eye and tail instead of midway between tip of snout and tail.

A good description of undoubted larvae of *Rana macrodon* is still to be written.

At metamorphosis this species is about 10 mm. long. The three smallest, completely transformed Bornean specimens measure 10.4, 12.8, and 12.8 mm. (FMNH 151480-1, 151492).

Ecological notes.—The ecological distribution of *macrodon* in Borneo has been discussed above (p. 168).

All specimens were caught on the banks of streams and none were seen away from the immediate vicinity of flowing water.

All Bornean localities for reliably identified *macrodon* lie within 200 meters of sea level. Mertens (1930) reports that *macrodon* is scarce below and common above 400 meters in Java and the Lesser Sundas. But because of the confusion between *blythi* and *macrodon*, a reliable comparison of altitudinal distributions using literature records is impossible.

The 27 adult Bornean females for which dates of collection are available were caught during the months April through August. The proportion of frogs having mature ova are: April 1/5, May 1/3, June 3/3, July 3/7, August 7/9. Presumably oviposition may occur in any of these months.

Geographic variation.—The Bornean samples of *macrodon* do not differ from one another in the characters studied. As a group, Bornean males differ from those of other samples in body proportions (Table 27), having longer legs (tibia to snout-vent ratio) and a shorter head than the other samples and a narrower head than Malayan males. Males from Siberut Island have the narrowest heads. Although the differences among the samples of females are not statistically significant, their body proportions follow the trends in the corresponding males.

TABLE 28.—Extent of web between two outer toes in *Rana macrodon*. Explanation in text, p. 164.

Sample	Proximal edge of tubercle	Center of tubercle	Distal edge of tubercle
	Number of individuals		
Borneo	31	22	1
Malaya	9	1	2
Siberut	8	1	0
Java	2	1	3

The web is slightly more extensive in Bornean and Javan frogs than in those from Malaya and Siberut (Table 28). In Table 28 the method of measuring the web used is as described above (p. 164).

Range.—As literature identifications of *macrodon* are suspect, the distribution given here is only of specimens examined. See also pp. 168–169.

Java, Sumatra, Siberut, Riouw Archipelago, Malay Peninsula as far north as Selinsing (4°53′ N), and Borneo.

SABAH: Beaufort District, Merabeh; Jesselton District, Jesselton; Kinabatangan District, Bukit Kretam; Labuan District, Labuan; Sandakan District, Sandakan, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tuaran District, Tuaran. SARAWAK: First Division, Kuching, Gunong Temiang; Second Division, Saribas; Third Division, Mengiong River, Fourth Division, Akah River, Labang, Niah, Patah River, Sungei Pesu, Tutoh River valley. KALIMANTAN: Pulau.

Rana microdisca Boettger

Material examined.—Java 7 (1 FMNH; 1 NHMW; 5 SNG); Lombok 1 (MCG); Mindanao *parva* 25 (2 FMNH; 23 SU); Palawan 35 (2 BM, types of *palavanensis*; 1 FMNH; 3 MCZ; 29 SU); Borneo 78+ larvae (4 BM; 54+larvae FMNH; 2 MCZ; 1 RMNH; 17 SM).

The Bornean populations of this wide-ranging species had been placed in a single subspecies, *R. m. palavanensis* (Inger, 1954A). Additional material from Borneo forces a change in my previous view.

The Bornean frogs fall into two sharply defined groups on the basis of tuberculation of the dorsal skin. Specimens (fig. 43A) from the eastern, lowland half of Sabah have many short ridges and warts dorsally, as far anteriorly as the upper eyelid. In this regard, they resemble Javanese *m. microdisca* (which, however, usually have rounded warts only) but are markedly different from frogs (fig. 43B) collected in western Sabah, Sarawak, and western Kalimantan. Frogs from the last three areas have smooth backs (except for the inverted V-shaped scapular tubercle typical of the entire group) and a thin, usually continuous dorsolateral fold. The dorsolateral fold in the eastern Bornean frogs invariably consists of a row of separated, elongated tubercles.

The western Bornean frogs are indistinguishable from Palawan specimens (except for a slight difference in size) and are placed in the subspecies *m. palavanensis*. The frogs from eastern Sabah differ from other populations of *microdisca* and are described below as the subspecies *m. finchi*.

Boulenger (1920) recognized these two Bornean forms, listing a specimen from Sandakan as *microdisca* and one each from Mount Penrissen, Sarawak, and from Mount Kina Balu as *palavanensis*.

Boulenger said that males of *palavanensis* had vocal sacs, but the only males available to him were from Celebes where *palavanensis*

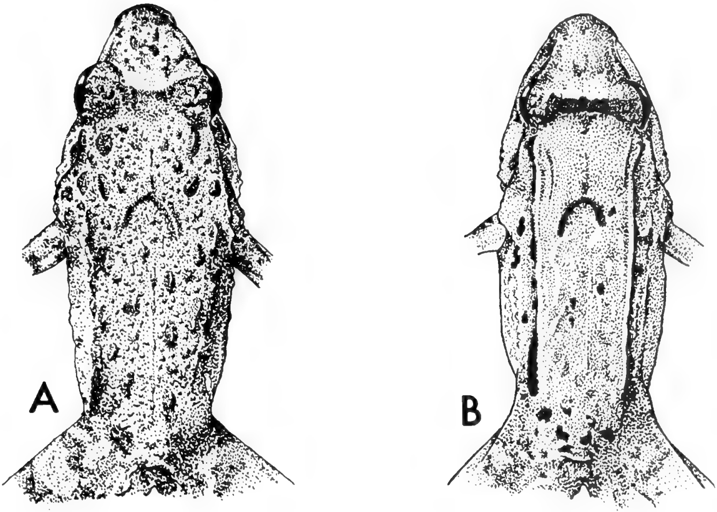


FIG. 43. *Rana microdisca finchi* (A) from eastern Sabah and *R. m. palavanensis* (B) from Sarawak.

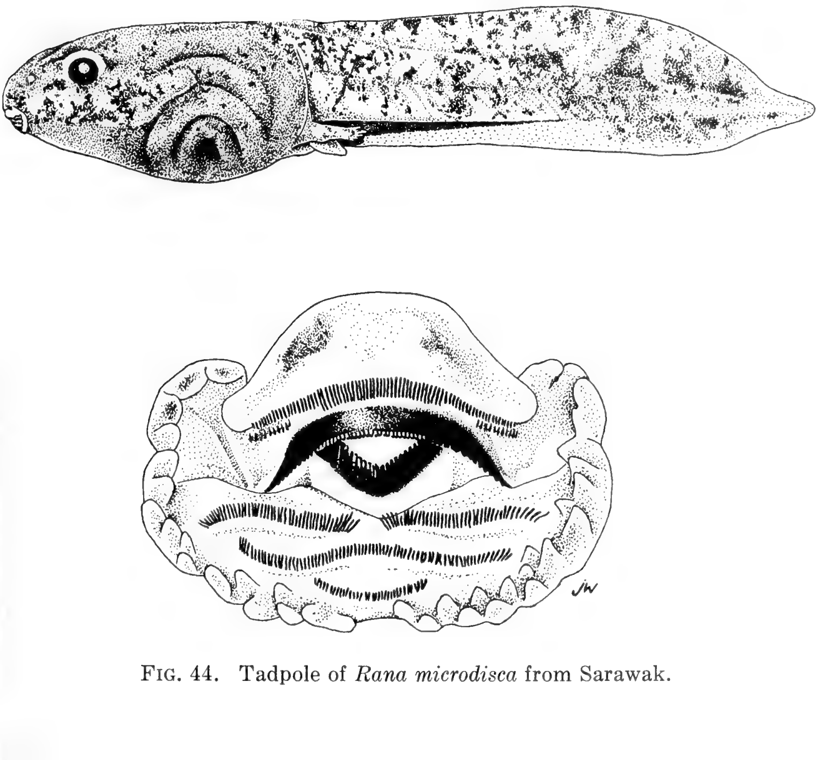


FIG. 44. Tadpole of *Rana microdisca* from Sarawak.

does not occur (Inger, 1954A). My Philippine paper erroneously followed Boulenger. Males of *palavanensis* from Palawan (7 examined) and from Borneo (4) do not have vocal sacs; these include one male (FMNH 148349) caught while calling.

The Philippine frog, *leytensis*, has been considered a subspecies of *microdisca* whereas *Rana parva* Taylor, which is sympatric with *leytensis* on Mindanao, has not (Inger, 1954A). Thanks to recent, intensive work in the Philippine Islands by Dr. W. C. Brown and Mr. Angel Alcala, it is possible to understand better the relations of *leytensis* and *parva* to one another and to other populations of the *microdisca* group.

As may be seen in Table 29, each form or population differs from the others in at least one character. These populations could be treated as separate subspecies in a Rassenkreis or as separate, but related species in an Artenkreis. Only in Mindanao do two forms occur together; both *leytensis* and *parva* are reported from Agusan and Davao provinces (Inger, 1954A), and Mr. Alcala has recently collected both in the Dapitan area of Zamboanga Province. The striking difference between *parva* and *leytensis* in almost all characters included in Table 29 cannot be interpreted as an example of recently developed character displacement (Brown and Wilson, 1955) as *leytensis* is almost as distinct from allopatric Bornean and Palawan populations as it is from sympatric *parva*. Furthermore, *leytensis* from Negros, where *parva* does not occur, are as distinct from all other forms as are *leytensis* from Mindanao. The morphological divergence of *leytensis* probably is the result of a long period of isolation from the rest of the stock.

Rana leytensis, usually living in the immediate vicinity of water, is ecologically as well as morphologically distinct from *parva* and the Bornean frogs.

Rana microdisca of Java is also more aquatic than *parva* and the Bornean populations. But morphologically the Javan frogs (and their larvae) are so similar to those of eastern Sabah that they must be considered conspecific. Each of these populations differs only slightly from Sarawak and western Sabah frogs, which in turn are taxonomically indistinguishable from Palawan frogs (*palavanensis*). *Rana parva* is only slightly different from *palavanensis* and is clearly conspecific with it.

The varying degrees of similarity among these populations suggest that *R. leytensis* is a distinct species and that the others are conspecific. The forms recognized here are:

R. microdisca microdisca—Java
R. m. dammermani—Lesser Sundas
R. m. palavanensis—Palawan and western Borneo
R. m. finchi—northeastern Borneo
R. m. parva—Mindanao

Dr. Brown has suggested in conversation that *Rana micrixalus* Taylor from Basilan and southwestern Mindanao is identical to *parva*. The only character that seemed to differentiate *micrixalus* from *parva* was the dorsolateral fold present only in *micrixalus* (Inger, 1954A). The dorsolateral surface varies in the fresh specimens of *parva* collected by Mr. Alcala. Whether the variation is genetic or is caused by preservation is unknown. But some of the *parva* (e.g., SU 20394) have a wide dorsolateral fold, as in *micrixalus*, and others have none. The range of variation in webbing of the new material of *parva* spans the slight difference between *parva* and *micrixalus* indicated by my previous descriptions (Inger, 1954A). *Rana micrixalus* is clearly a member of the *microdisca* Artenkreis. Whether or not *micrixalus* is a distinct subspecies can only be determined by examining fresh material.

Frogs of this Artenkreis also occur on Celebes (Inger, 1954A). Males have vocal sacs and bony mandibular processes as in *R. leytensis*. Probably this population (or populations) represents another distinct species.

A decision on the taxonomic level to assign to each of these populations must be subjective to a certain extent. Only in the case of the *leytensis-parva* pair does sympatry provide an objective criterion. The decisions in all of the allopatric pairs depend on judgments arrived at by comparison of the morphological differences between other closely related, sympatric species of *Rana*.

Despite this taxonomic problem, the close relationships of these populations are clear. The various degrees of similarity suggest an evolutionary history along the following lines.

First stage: An aquatic frog similar to *leytensis*; males with vocal sacs. Probably widely distributed in Sundaland; certainly present in Borneo. Population spreads into Philippine Islands.

Second stage: Philippine population(s) isolated. Sundaland form loses vocal sacs; becomes similar to *m. microdisca*; still aquatic.

Third stage: Philippine population still isolated. Sundaland probably fragmented in this stage isolating populations in Java (*m. microdisca*) and Lesser Sundas (*m. dammermani*). In Borneo stock becomes semi-terrestrial or terrestrial.

TABLE 29.—Geographic variation in frogs of the *Rana microdisca* Artenkreis.

Locality	Form	Back	Fifth toe (lateral edge)	First toe (median edge)	Fourth toe (phalanges free)	Vocal sac	Mandibular odontoids
Mindanao	*leytensis*	warty	wide flap	narrow flap or ridge	2	present	present
Mindanao	*parva*	smooth	ridge	smooth	3½	absent	absent
Palawan	*palavanensis*	smooth	ridge	smooth	3	absent	absent
Western Borneo	*palavanensis*	smooth	ridge	smooth	2–2½	absent	absent
Northeastern Borneo	*finchi*	warty	narrow flap	smooth	2½	absent	absent
Java	*microdisca*	warty	ridge	smooth	2½	absent	absent

TABLE 29.—Geographic variation in frogs of the *Rana microdisca* Artenkreis (*Continued*)

Snout-vent (mm.) Males	Snout-vent (mm.) Females	Clutch size	Mature ova: Mean[1] size of ova	Mature ova: Color[2]	Color of lips	Larval dentition
34.3–48.6 m[5]=41.34 N=37	39.0–57.6 m=46.34 N=36	44–62[3] N=7	15.0[4]	B & W[4]	barred, brown and white	I/1–1:II[3]
24.9–27.9 m=26.00 N=11	26.6–29.4 m=28.03 N=6	8–13 N=3	17.8	B & W	brown, uniform or with small white dots	—
25.8–29.7 m=27.91 N=7	28.3–33.8 m=31.19 N=11	8–15 N=4	16.3	B & W	brown with large white spots	—
27.0–29.6 m=28.3 N=2	35.5–39.4 m=37.18 N=4	—	—	—	brown with large spots; or barred brown and white	I:1–1/1–1:II
32.1–39.0 m=35.12 N=9	38.8–42.4 m=40.98 N=6	14–57 N=3	15.2	B	barred, brown and white	I:1–1/1–1:II
32.5–39.0 m=35.57 N=3	36.9–42.7 m=40.33 N=3	—	—	—	barred, brown and white	I:1–1/1–1:II

[1] In ocular micrometer units; 8 units=1.0 mm.

[2] B & W=blackish brown animal hemisphere, whitish vegetal hemisphere; B=both hemispheres, dark brown.

[3] Data from Negros frogs (Alcala, 1962). [4] Data from Negros frogs in FMNH. [5] m=mean.

Fourth stage: Continuing differentiation within Borneo. Semi-terrestrial frogs invade Palawan and Mindanao. New invader (*parva*) of Mindanao ecologically differentiated from earlier one (*leytensis*). Old invader unable to move back to Borneo, probably because of competition with more advanced (or vigorous) ecological equivalents (e.g., *Rana kuhli* and *R. paramacrodon*).

Description.—Body and limbs neither stocky nor slender; head slightly longer than broad; tympanum distinct, usually two-thirds eye diameter; vomerine teeth in oblique rows, between and behind choanae; an inverted V-shaped tubercle between shoulder; otherwise mid-dorsum smooth or with numerous round and elongated tubercles; dorsolateral fold continuous or interrupted.

Fingers bluntly rounded; tips of toes distinctly expanded into round disks lacking circummarginal grooves, but have a dorsal longitudinal depression; web reaching or narrowly missing disks of first three toes on outer edges and of fifth toe on inner edge; two to three phalanges of fourth toe free of web; fifth toe usually with a ridge of skin laterally; first metatarsal without ridge or flap of skin on inner border.

Color (in life) brown or reddish brown above; interscapular tubercle black; rest of mid-dorsum immaculate or with a few black spots; limbs with dark crossbars; ventrally immaculate white or with dark brown spots anteriorly; a few individuals with a light vertebral stripe and a narrow light line on the inner edge of the tibia.

Secondary sex characters.—Males of the Bornean populations lack vocal sacs, nuptial pads, and bony mandibular processes.

In the absence of striking secondary sex characters, the onset of sexual maturity in males is difficult to establish. Of 11 males from northeastern Borneo, two are 25.1 and 26.3 mm., snout to vent, and nine are tightly clustered between 32.1 and 39.0 mm. (mean 35.12 ± 0.70 mm.). Enlarged ova provide an indicator of maturity in females. Those from eastern Borneo containing mature ova range from 38.8 to 42.4 mm. (mean 40.98 ± 0.52 mm.; $N = 6$). Just three mature females from northwestern Borneo were examined; their size range is 36.8–39.4 mm. The four adult males seen from northwestern and western Borneo measure 27.0–29.6 mm. Thus males from both populations are smaller than sympatric females.

Larvae.—The following description is based on 36 larvae (fig. 44) in stages from incomplete closure of the operculum to partial resorption of the tail.

Body oval, width about three-fourths length; somewhat flattened above; eyes and nostrils dorsolateral; interorbital and internarial width subequal, equal to nostril-snout, but longer than eye-nostril; oral disk ventral, subterminal, less than one-third width of head, slightly narrower than interorbital; upper lip very short, bordered by one row of labial teeth; thick papillae in a single row at lateral corners of upper lip and around lower lip; usually with a very narrow gap at center of lower lip; labial teeth I:1+1/1+1:II (14 specimens) or I/1+1:II (2 specimens); inner upper row with a very wide gap; inner lower row with a narrow gap; two inner lower rows subequal, outermost row one-third or less length of others; beaks finely serrated, black in distal third.

Spiracle sinistral, tubular, in line between eye and insertion of hind limb and equidistant between them; anus dextral, opening at edge of ventral fin.

Tail 0.54–0.65 of total, margin weakly convex, abruptly tapering near end with tip attenuated; dorsal fin rising gradually from root of tail, reaching maximum depth at beginning of last quarter, greater than depth of caudal muscle in distal third; ventral fin slightly more than half depth of dorsal one, margin almost straight.

Color (in alcohol) above brownish, below colorless; an obscure transverse dark bar just anterior to root of tail, another across top of caudal muscle near base; caudal muscle and dorsal fin densely speckled with melanophores; a row of large black spots on dorsal surface of caudal muscle; ventral fin speckled in distal third only. In advanced larvae (ca. Stage XVII–XX) the dorsal surfaces of the hind limbs and the back become very dark.

In advanced larvae (Stages XVII, XVIII), the tips of the toes are expanded into small but distinct disks; the first three toes webbed to the disks on the outer edges and the fifth toe to the disk on the inner edge; on the inner edges the second toe webbed to the subarticular tubercle and the third toe to the distal subarticular tubercle; fourth toe webbed to distal subarticular tubercle; inner metatarsal tubercle oval; no outer metatarsal tubercle visible; a ridge of skin along outer edge of fifth toe. Head-plus-body lengths of four larvae in these stages are 8.8–9.9 mm., total length 15.7–18.9 mm.

The feet in a specimen with fore limbs erupted (Stage XX) and in one with the tail partially resorbed (Stage XXIII: snout-vent 8.7 mm., tail 4.5 mm.) are identical to the preceding description. The tips of the fingers are not as wide as those of the toes and are only slightly wider than the basal phalanges. The first finger is subequal

to the second, which equals the fourth. No fringes of skin are present on the fingers. The Stage XX individual has faint indications of dorsolateral folds, which are well developed in the Stage XXIII froglet. The latter also has weakly developed middorsal ridges.

The webbing, digital tips, tubercles, and dorsolateral ridges of these advanced larvae, all of which are from Sarawak, agree with young, transformed *microdisca*. The latter is the only known Bornean *Rana* having terminal disks on the toes but not on the fingers and having the second and third toes only half webbed on the inner margins.

The above description agrees with those of Smith (1927), Dunn (1928), Mertens (1930), and Schijfsma (1932) for various forms of *microdisca* from Celebes, Java, the Lesser Sundas, and Java, respectively. In one character, however, the present sample differs from all the others, namely, the attenuated tip of the tail. The above authors refer to obtusely pointed tails in their larvae.

The series (FMNH 63514-15) identified earlier (Inger, 1956, p. 404) as *m. palavanensis* is almost assuredly some other species of *Rana* of the same species group, perhaps *paramacrodon*. The webbing appears to be slightly more extensive than in the above description and the tail tapers gradually to an obtuse point. This is not a case of geographic variation, for two tadpoles (FMNH 63518) having the tail form I now attribute to *palavanensis* were collected in the same area of Sabah.

Ecological notes.—In Borneo this species is a characteristic form of the forest floor, being especially abundant in low, swampy areas. At Deramakot in the Kinabatangan basin eight frogs were collected in the flat areas subject to periodic flooding but only one on the isolated ridges. At Kalabakan, where no swampy areas exist, only three frogs were obtained in one month as compared to the nine caught at Deramakot in the same length of time and the 11 in the low-lying Sepilok Forest Reserve in five days. All of these frogs are *R. m. finchi*.

In Sarawak *m. palavanensis* shows the same ecological distribution, being more frequently encountered in flat, marshy areas than on slopes.

Altitudinal distribution within Borneo is extensive. All frogs from northeastern Borneo were caught within 75 meters of sea level. In the north and west of the island, though *microdisca* has been collected within a few meters of sea level, many specimens have come from 900 to 1400 meters above sea level. In Java and the Lesser

Sundas *microdisca* is rarely if ever found below 1000 meters (Mertens, 1930, 1934).

The reproductive habits of *microdisca* are unusual for *Rana*. The adult male holotype of *R. m. finchi* was collected at night in a small rain pool on a road through a logged area. The frog was near the edge of the pool when first observed and its back, which was out of the water, was covered with small tadpoles 9–10 mm. long. As the frog was picked up, several larvae wriggled off into the water. In the absence of a proper container, the live frog was wrapped in a banana leaf and brought back to the field laboratory. Some of the larvae either had been dislodged or had wriggled off the adult's back. Eighteen were in sufficiently good condition to warrant preservation. In terms of bulk the 18 probably represented half of the original number on the adult.

About half of these larvae had the operculum closed on the right side but not on the left (i.e., Stage 24, Shumway, 1940); in the remainder the operculum was closed on the left (Stage 25). The beaks were present and faintly edged with black; no labial teeth were evident. The gut had one or 1½ coils.

The association, both physically and taxonomically, with the adult is certain. The frog and the larvae were tagged immediately upon arrival in the laboratory and the tails of the tadpoles have the dark crossbars characteristic of the older *microdisca* larvae described above.

The male has no apparent specialization for carrying the larvae other than the numerous dorsal glandular folds that probably secrete mucous. Earlier in development, the larva may have clung to the adult by means of the suckers, but in the stage at which they were collected the suckers were no longer visible. If, as seems likely, the male was transporting the tadpoles to water, the action may be timed to coincide with the loss of the suckers.

Males call on the forest floor at some distance from water.

Geographic variation.—This species varies in the form of the dorsolateral fold, in dorsal pattern, and in the arrangement of the vomerine teeth as well as in the characters shown in Table 29.

The dorsolateral fold is interrupted in *R. m. finchi*, continuous in *R. m. palavanensis* and probably in *R. m. parva* (see above, p. 212), and represented by widely separated tubercles in *R. m. microdisca*.

Both *m. microdisca* and *m. finchi* usually have dark spots scattered over the back in addition to the dark interorbital bar and the dark

scapular V. Dorsal markings are restricted to the interorbital and scapular ones in *m. palavanensis* and *m. parva.*

In most populations of *microdisca,* the vomerine tooth patches are separated by a distance at least equal to one-half of the length of one patch. In *m. finchi* and *m. dammermani* (Mertens, 1930) the groups of teeth are much closer together and in *finchi,* at least, may actually touch medially.

The subspecies occurring in Borneo are as follows.

Rana microdisca palavanensis (Boulenger). Figure 43B.

Rana palavanensis Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14,** p. 85—Palawan; 1920, Rec. Ind. Mus., **20,** p. 59 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 182 (part); Smith, 1925, Jour. Sarawak Mus., **3,** p. 32.
Rana microdisca palavanensis Inger, 1954, Fieldiana: Zool., **33,** p. 299 (part).

Material examined.—Palawan 35 (2 BM, types of *palavanensis*; 1 FMNH; 3 MCZ; 29 SU); Borneo 44+2 lots of larvae (4 BM; 20+larvae FMNH; 2 MCZ; 1 RMNH; 17+larvae SM).

Diagnosis.—Dorsolateral folds continuous; mid-dorsum usually smooth except for inverted V-shaped tubercle between shoulder; a ridge of skin along lateral margin of fifth toe; no ridge or flap of skin along inner edge of first metatarsal; groups of vomerine teeth separated by at least half the length of one group; underside of body immaculate; lips brown usually spotted with yellow or white.

Color (in life) dark brown above with black markings; dorsal surfaces of tibia and tarsus reddish brown; chest and abdomen lemon yellow, with tinge of orange posteriorly; ventral surfaces of thighs and tibia orange or orange-yellow.

Range.—Palawan, western Sabah, Sarawak, and Kalimantan.

SABAH: Kota Belud District, Mount Kina Balu. SARAWAK: First Division, Lundu, Mount Penrissen, Mount Gadin (Smith, 1925B); Third Division, Baleh River, near mouth of Putai River, Sungai Menuang Ili at headwaters of Baleh River, Mengiong River; Fourth Division, Patah River. KALIMANTAN: Mount Semedum.

Rana microdisca finchi[1] new subspecies. Figure 43A.

Holotype.—Field Museum of Natural History number 77499, an adult male from Kalabakan, Tawau District, Sabah. Collected June 28, 1956, in secondary growth by Robert F. Inger.

[1] Named for O. C. Finch to whom I am indebted for much assistance and pleasant companionship in the field.

Diagnosis.—Dorsolateral folds interrupted; numerous mid-dorsal ridges and tubercles; a narrow flap of skin along lateral margin of fifth toe; no ridge of skin along first metatarsal; groups of vomerine teeth separated by less than half the length of one group; throat mottled; lips barred.

Description.—Like description under *microdisca* above, except for characters mentioned in preceding diagnosis.

Measurements of holotype (mm.).—Snout-vent 35.1; head width 13.1; head length 13.9; tibia 19.6.

Paratypes.—All from Sabah. Field Museum of Natural History 63297, 63350, 76570, 76575–76, 76579–81, 76583–88, 76592–93, 76597–99, 76601, 76603–04, 76626, 77497, 77564 (larvae).

Eight unsexed juveniles vary in length between 14.7 and 26.6 mm. Two males measure 25.1 and 26.3, and nine others, including the holotype, 32.1–39.0 (mean 35.2 ± 0.70 mm.). Head width varies from 0.35 to 0.39 of snout-vent (median 0.373; $N=16$) and head length from 0.36 to 0.41 (median 0.392; $N=15$). The tibia as a proportion of snout-vent varies from 0.53 to 0.61 (median 0.562; $N=16$).

Comparisons.—See *Geographic variation* above.

Range.—Eastern half of Sabah.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Sandakan District, Sandakan, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tawau District, Kalabakan.

Rana nicobariensis Stoliczka

Hylorana nicobariensis Stoliczka, 1870, Jour. Asiatic Soc. Bengal, **39**, p. 150, pl. 9, fig. 2—Nicobar Islands.

Rana nicobariensis Boulenger, 1885, Ann. Mag. Nat. Hist., (5), **16**, p. 389; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 224; Smith, 1925, Sarawak Mus. Jour., **3**, p. 33; 1931, Bull. Raffles Mus., no. 5, p. 9.

Rana nicobariensis nicobariensis Inger, 1954, Fieldiana, Zool., **33**, p. 331; 1956, *idem.*, **34**, p. 406.

Rana macularia var. *javanica* Horst, 1883, Notes Leyden Mus., **5**, p. 243.

Rana nicobariensis javanica Mertens, 1930, Abh. Senck. Naturf. Ges., **42**, p. 110.

Material examined.—Borneo 80+6 lots of larvae (69+larvae FMNH; 11 NSH); Mentawei Ids. 34 (2 BM; 32 SNM).

Description.—Body and legs slender; head elongate, width 0.26–0.30 of snout-vent, length 0.36–0.39; snout pointed, much longer than eye, projecting in profile, nostril behind level of symphysis but much

nearer to tip of snout than to eye; interorbital equal to or wider than upper eyelid; eye diameter slightly greater than eye-nostril distance; tympanum conspicuous, three-fourths to four-fifths eye diameter, 0.07–0.09 of snout-vent; vomerine teeth in two oblique groups between choanae, distance between groups equal to length of single group but greater than distance between tooth patches and choanae.

Finger tips dilated into small subequal disks having horizontal circummarginal grooves, disks scarcely twice diameter of phalanges,

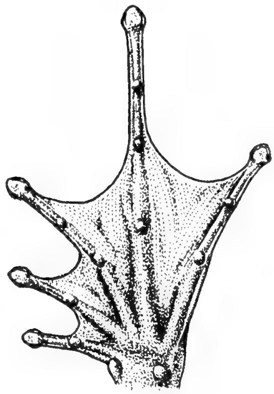


FIG. 45. Ventral view of foot of *Rana nicobariensis*.

less than half width of tympanum; first finger equal to or longer than second; inner margin of third finger rarely with a narrow dermal fringe, other fingers never with fringes; a supernumerary tubercle on each of three outer metacarpals. Tips of toes with disks larger than those of fingers; web (fig. 45) reaching midway between subarticular tubercles and terminal disks on outer edges of first three toes, usually closer to disk on inner edge of fifth; fourth toe with 2½ to three phalanges free of broad web; a small oval inner metatarsal tubercle and a conspicuous round outer one; heels overlapping when flexed limbs held perpendicular to body, tibia 0.50–0.58 of snout-vent.

Dorsal and lateral skin granular; narrow dorsolateral glandular fold present; several horizontal glands behind rictus; no fold from eye to axilla; skin of venter smooth.

Color (in life) pale brown above with obscure dark spots; sides usually darker brown, especially on side of head; upper lip white; whitish below with a few grayish spots. Color in preservative much the same; some frogs with very dark throats; hind limbs with dark crossbars.

In habitus and size *nicobariensis* is similar to *Rana chalconota* and *Amolops jerboa* but is easily distinguished from them by the less extensive webbing. The first three toes and the fifth are broadly webbed to the disks in *chalconota* (fig. 34) and *jerboa* but not in *nicobariensis* (fig. 45).

Secondary sex characters.—Female *nicobariensis* are about 8 mm. larger than adult males. Snout-vent range of Bornean females is 46.5 (the smallest having mature ova) to 53.2 mm., and the mean of 19 is 50.11 ± 0.44 mm. Thirty-one Bornean males having nuptial pads vary from 37.2 to 46.5 mm. and have a mean of 42.77 ± 0.48 mm.

Minor sexual differences appear in body proportions. In the following discussion the first ten frogs of each sex drawn from the container were compared by means of the Mann-Whitney U test. The tympanum is larger in males, although the difference is not evident from gross inspection. The tympanum is 0.076–0.090 of snout-vent (median 0.084) in males and 0.072–0.083 (median 0.078) in females; the difference is statistically significant ($U = 17.5$; $P = 0.02$). The head is slightly longer in males. Head length is 0.361–0.393 of snout-vent (median 0.375) in males and 0.357–0.378 (median 0.365) in females; this difference is also statistically significant ($U = 20.5$; $P = 0.03$). Females have longer tibias, the range of this proportion being 0.519–0.581 (median 0.538) in females and 0.504–0.556 (median 0.517) in males. The difference is significant at the 0.01 level ($U = 15$).

All the Bornean males examined have paired subgular vocal sacs with round openings on each side of the mouth. The gular skin overlying the sacs is only slightly wrinkled. The nuptial pad is a yellowish velvety structure occupying the dorso-medial surface of the first finger from its base to the level of the subarticular tubercle. The pad is constricted in the center and in five of 31 males is divided at that point. Males also have very feeble translucent asperities on the chin and much stronger ones on the dorsal surfaces of the head, trunk, and hind limbs. A pink linea masculina forms the dorsal border of the obliquus muscle. The humeral gland in all of these males is large, covering almost the entire anterior surface of the upper arm.

Larvae.—Thirty-two larvae (fig. 46), from pre-limb bud to metamorphic stages, were collected. The older larvae have the distinctive webbing and other characters of adult *nicobariensis*, which were caught at the same pools. These tadpoles have the long papillae figured by Schijfsma (1932). Smith's (1930) larvae, which have seven rows of labial teeth on each lip and large dermal glands, are clearly not *nicobariensis*. The developmental sequence at hand is so complete that the identification can be considered certain.

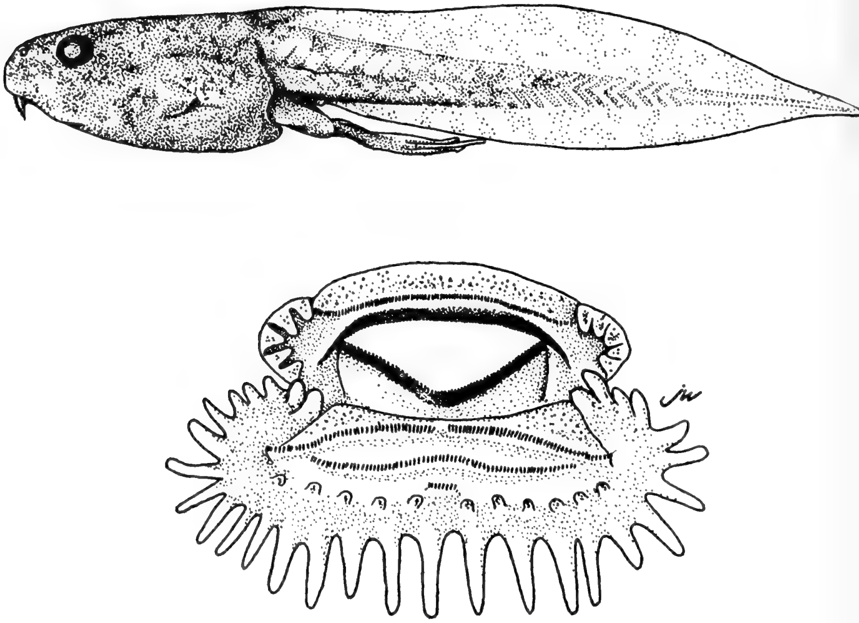


FIG. 46. Tadpole of *Rana nicobariensis* from Sabah.

Body oval, width 1⅓ times in length; eyes dorso-lateral, not visible from below; nostrils dorsal, mid-way between eye and tip of snout; internarial distance equal to eye-nostril, but shorter than interorbital; oral disk ventral, terminal, one-half width of head; papillae in two continuous rows on edge of lower lip; inner papillae short, outer ones long, about half width of mouth openings; beaks narrowly edged with black; labial teeth I/1–1: I (2), I/1–1: II (27); the outermost lower tooth row one-third to one-fourth of inner rows. Spiracle sinistral, tubular, visible from above and below, closer to root of hind limb than to eye; anus dextral, tubular.

Tail 0.57–0.67 of total length, with convex margins, tapering gradually in last third to rounded point; dorsal fin deeper than caudal muscle for two-thirds of tail length; ventral fin about half depth of dorsal, slightly less than depth of caudal muscle.

No glandular patches on head or body.

Color of pre-limb bud stages pale with dark bars on head; as tadpoles age body loses transparency and becomes mottled with brown; beyond Stage X both fins and caudal muscle with dark network.

Sizes and tail proportions at various stages are given in Table 30.

TABLE 30.—Size and tail proportion at various developmental stages (after Taylor and Kollros, 1946) of larval *Rana nicobariensis*.

Stage	No.	Total length	Tail/Total length
pre-limb bud	2	11.8	—
I–V	5	16.4–25.0	0.573–0.612
XI–XIII	3	27.8–29.5	0.616–0.646
XVII–XVIII	5	41.9–47.7	0.637–0.670
XX	1	39.1	0.616

Ecological notes.—In coastal towns of Sabah, *Rana nicobariensis* is probably the most conspicuous frog, not because it is seen but because its harsh clacking call can be heard all through the day coming from roadside ditches, cisterns, and low, damp areas. It never occurs in virgin forest or even in dense secondary growth. At Bukit Kretam, which is within ten miles of the coast, adults were heard and seen along a tiny stream where it flowed through the large camp clearing. They were not observed at the edge of the clearing in the shady tangle made by small trees and shrubs. Similarly, at Kalabakan, which is also within ten miles of the sea, *nicobariensis* occurred only in large camp clearings that were bare of trees. There *nicobariensis* lived in damp grassy patches or in rain-filled depressions made by tractors and where not even grass was growing. All larvae were caught in pools in clearings.

Significantly *nicobariensis* was not observed in the Deramakot camp clearing. This large clearing, which was essentially like those at Bukit Kretam and Kalabakan, was less than a year old at the time of my visit (1956), but it is separated from the coast by 70 miles largely covered then by virgin rain forest. Other Bornean localities for *nicobariensis* (e.g., Bongon, Kiau, Sandakan, and the Kelabit Plateau) are old areas of human concentration where the original vegetation has long been destroyed and large clearings are common.

Most Bornean records are within 100 meters of sea level. Its presence at Kiau (925 meters) and on the Kelabit Plateau (1000–1150 meters) show that *nicobariensis* is not restricted to low elevations over most of Borneo because of an inability to tolerate the climate of higher levels. Its scarcity at high altitudes seems to result either from the isolation of suitable biotopes or from the absence of suitable biotic conditions (see p. 371). Van Kampen (1923) cites records as high as 1430 meters in Sumatra and 1500 meters in Java.

All Bornean females but one were collected during the month of June; 14 have enlarged and pigmented ova, two have only very small

immature ova, and two have ova in an intermediate stage. One caught in October had ova in the oviduct. Twenty-nine males were obtained during June (1950, 1956) and all have fully developed secondary sex characters. One male collected in April, one in July, one in August, five in October, and one in November also have the sex characters developed. Three series of larvae were collected in June (1950, 1956). Thus active breeding occurs in June and may extend at least from April to November.

Range.—*Rana nicobariensis* occurs from southern Thailand (Smith, 1930) to Bali (Mertens, 1930) and Palawan (Inger, 1954A).

SABAH: Jesselton District, Jesselton; Kinabatangan District, Bukit Kretam; Kota Belud District, Kiau (Smith, 1931A); Kudat District, Bongon (Boulenger, 1920); Lahad Datu District, Lahad Datu, Silabukan valley; Sandakan District, Sandakan; Tawau District, Kalabakan; Tuaran District, Tuaran. SARAWAK: Fourth Division, Bario, Pa Main, Pa Umur; Fifth Division, Trusan River (Smith, 1925B). KALIMANTAN: Kapuas Barito District, Buntok (Witte, 1933).

Rana paramacrodon new species

Holotype.—Field Museum of Natural History number 76883. An adult male from the Sungei Tawan, a small tributary of the Kalabakan River, Tawau District, Sabah, collected June 23, 1956, by Robert F. Inger.

Diagnosis.—A moderate-sized *Rana* (to about 75 mm., snout-vent) of the ranae grunnientes group of Boulenger (1920); a dark rhomboidal mask covering tympanum except lower rim; fourth toe with two phalanges free of web; usually without a continuous dorsolateral fold; males with enlarged heads and mandibular processes but without nuptial pads.

Description of holotype.—Body moderately stocky; legs heavy; head depressed, longer than broad; snout obtusely pointed; canthus rostralis distinct, but rounded; lores oblique, slightly concave; nostril closer to tip of snout than to eye; eye moderate, horizontal diameter equal to eye-nostril distance; interorbital wider than eyelid; tympanum distinct, subequal to eye diameter; vomerine teeth in oblique, prominently raised groups, groups narrowly separated, extending beyond level of choanae; tongue narrow anteriorly, deeply notched.

Fingers with blunt tips; first finger much longer than second, fourth longer than second; subarticular tubercles moderate; palmar

tubercles feeble; a distinct fold of skin on inner edges of second and third fingers. Toes with distinctly swollen tips; disks without circummarginal grooves but with a median longitudinal groove on dorsal surfaces; third toe extending just beyond fifth; first three toes broadly webbed to disks on outer edges; fifth toe broadly webbed to disk; fourth toe broadly webbed to distal subarticular tubercle, narrowly so to base of disk; second and third toes narrowly webbed to disks on inner edges; excision of membrane between two outer toes reaching proximal to middle subarticular tubercle of fourth when toes are in contact; a broad flap of skin along outer and inner edges of foot; subarticular tubercles prominent, round or oval; inner metatarsal tubercle prominent, elongate, shorter than first toe, no outer metatarsal tubercle.

Skin above coarsely shagreened, one or two feeble longitudinal ridges in scapular region; a cluster of pustules on rear half of upper eyelid; a strong supratympanic fold from eye to arm insertion; dorsal surfaces of legs with a few white-tipped tubercles; ventral surfaces smooth.

Color (in alcohol) dark brown above with a light rust-colored interorbital bar and a narrow, light, vertebral line; sides of head (fig. 47) lighter; three broad grayish-brown labial bars separated by narrow whitish interspaces; a dark brown rhomboidal spot covering all except lower rim of tympanum; dorsal surfaces of limbs slightly lighter than back with dark crossbars; tibia with narrow light line on dorso-median edge; throat grayish; chest, abdomen, and ventral surface of legs white. In life temporal spot black, posterior half of abdomen and ventral surface of legs yellow.

Measurements (mm.): snout-vent 73.2; head length (to rear of commissure) 32.0; head width 27.6; tympanum 6.2; tibia 37.4, foot 35.8.

Paratypes.—FMNH 76605–07, 76609, 76614–16, 76620, 76623, 76628, 76884–86 from the type locality; 76631–32, 76881 from small tributaries of Kalabakan River, respectively one and two miles upstream from Sungai Tawan, the type locality; FMNH 76577–78, 76582, 76831 from Sepilok Forest Reserve, Sandakan District, Sabah; FMNH 14279 Sandakan, Sabah; FMNH 128223–4, 129145 from Niah, Fourth Division, Sarawak; NSH unnumbered, Kota Belud, Kota Belud District, Sabah.

These range in size from 31.9 to 72.8 mm.; only six are smaller than 50 mm. All have the distinctive temporal spot covering the tympanum, the broad labial bars, and the grayish throats. In life

all of the Kalabakan frogs had the yellowish ventral coloration described under the holotype; unfortunately no observations on this point were made for the Sepilok frogs and, since the yellow fades rapidly in preservative, agreement with the holotype in this character is indeterminable. Seven of the 21 paratypes have a light stripe on the vertebral region and on the tibia; in one of them the vertebral marking is broad.

The webbing is remarkably uniform in this series and agrees with the holotype. Variation is most conspicuous in the dorsal skin. A few specimens have a series of short and narrow ridges in the dorsolateral region, but these do not form a dorsolateral fold. Others have short oblique ridges in the scapular region though none has an inverted V such as appears in other species of this group. The tibia varies from 0.49 to 0.55 of the snout-vent length, and the foot (measured from the base of the metatarsal tubercle) is slightly shorter in all but two specimens though the range (0.47–0.55 of snout-vent) is much the same.

Secondary sex characters.—Sexual maturity evidently is reached by females at about 55–60 mm. Three females (50.9–53.5 mm.) have straight or slightly kinked, but not enlarged, oviducts. Three (54.5–61.5 mm.) have kinked, enlarged oviducts but immature ova. One measuring 56.1 mm. and seven others (60.9–66.2 mm.) have enlarged pigmented ova. Judging by the development of the mandibular processes (see below), the five males (59.4–73.2 mm.) are mature. Three of the last are larger than 70 mm., indicating that males reach a slightly greater length than females.

Males of this form (see below) lack vocal sacs and nuptial pads. Their heads show the increase in length characteristic of males of this species group (Inger, 1954A). The head length (measured from the commissure of the jaws) to snout-vent ratio varies in the five males from 0.41 to 0.44 (mean 0.425 ± 0.004) and in the eleven females from 0.40–0.42 (mean 0.406 ± 0.002). No sex dimorphism in the relative width of the head is apparent, the ranges for the head width to snout-vent ratio being 0.36–0.38 (males) and 0.35–0.38 (females).

As in other species of this group, a bony process develops at the anterior end of the mandible in males. Females and juvenile males have a triangular enlargement whose relative size remains roughly constant. As the male becomes mature, the core of the process elongates into a tooth-like projection. Measuring from the ventral edge of the mandible to the tip of the mandibular process, the ratio of

process length to snout-vent varies in males from 0.043 to 0.059 and in females from 0.033 to 0.038.

Ecological notes.—All seventeen frogs from the Kalabakan drainage were caught at night along clay and gravel banks of small (about three meters wide) streams in primary rain forest. Associated with them in these places were *Rana blythi, R. kuhli, R. signata, R. chalconota, Bufo asper,* and *Pedostibes hosei.*

The five obtained in the Sepilok reserve were collected, together with *R. macrodon* and *R. blythi,* at night on clay banks of a small stream in the camp clearing. The reserve consists of selectively logged rain forest having a well-developed high canopy and small patches of virgin forest. All of the known localities are less than 100 meters above sea level.

Remarks.—A small frog from western Borneo, though clearly conspecific with these from Sabah and northern Sarawak, is distinct enough to warrant recognition as the subspecies *Rana paramacrodon kenepaiensis,* described below.

Comparisons.—Although in this discussion the comparisons are made with the typical, that is the Sabah and Sarawak form, *paramacrodon paramacrodon,* the only statements that do not hold good for *p. kenepaiensis* are those relating to vocal sacs.

Superficially similar to half-grown *Rana macrodon* and *R. blythi, paramacrodon* is distinguished from them by its smaller size, by the extent of its tympanic mask, by its reduced webbing, and by its ventral coloration. Many but not all specimens of *macrodon* and *blythi* have a dark streak across the upper third of the tympanum, but never have a complete mask like that of *paramacrodon.* The posterior third of the abdomen and the ventral surfaces of the hind limbs of living *macrodon* and *blythi* are always white or ivory whereas these surfaces are yellow in *p. paramacrodon.* The fourth toe in *macrodon* and *blythi* is broadly webbed to the disk; that of *paramacrodon* has two phalanges free of broad webbing. On the inner edges of the second and third toes the web reaches the disks as a broad sheet in the large species, but only as a narrow fringe in *paramacrodon.*

The most interesting difference between *blythi* and *paramacrodon* involves egg pigmentation. Enlarged (2 mm.) ova of *paramacrodon* have a densely pigmented hemisphere, such as is characteristic of most species of *Rana,* but those of *blythi* are a uniform yellowish gray color.

Of the Philippine forms related to *macrodon* and *modesta, magna, macrocephala, acanthi,* and *visayanus* have more extensive webbing

than *p. paramacrodon*, lack the tympanic mask, and have vocal sacs. *Rana woodworthi*, of the northern Philippine Islands, has a tympanic mask like *p. paramacrodon* and is similar in size, but has a dorsolateral fold, vocal sacs, and more extensive webbing.

Both *p. paramacrodon* and *p. kenepaiensis* have more extensive webbing than *Rana leytensis*. The differences are especially conspicuous along the inner edge of the second toe (which is narrowly webbed

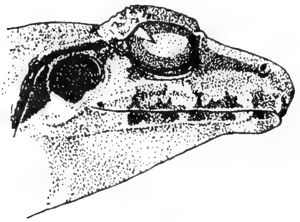


FIG. 47. Side of head of *Rana paramacrodon*.

to the disk in *paramacrodon* but not in *leytensis*), the inner edge of the first metatarsal (bearing a flap in *paramacrodon*, at most a ridge in *leytensis*), and the inner edge of the third finger (bearing a distinct flap in *paramacrodon* and a weaker one in *leytensis*). Though *leytensis* has a dark tympanic spot, it is narrow like that of *R. blythi* (fig. 30Q) and not full as in *paramacrodon* (fig. 47). Finally, the finger tips of *leytensis* are distinctly swollen whereas those of both forms of *paramacrodon* are not.

Rana modesta is distinguished from *p. paramacrodon* by broader webbing, by the absence of a tympanic mask, and by the presence of vocal sacs.

Range.—This form is known only from Sabah and northern Sarawak.

SABAH: Kota Belud District, Kota Belud; Sandakan District, Sandakan, Sepilok Forest Reserve; Tawau District, Kalabakan. SARAWAK: Fourth Division, Niah; Sungei Pesu.

Rana paramacrodon kenepaiensis new subspecies

Holotype.—Rijksmuseum van Natuurlijke Historie, Buttikofer Expedition no. 20 from Merkata, Kenepai Mountains, western Kalimantan. Adult male collected December, 1893, by J. Buttikofer.

Diagnosis.—Differing from the typical form in being smaller, in having vocal sacs, and in having slightly longer hind legs.

Description of holotype.—Like the typical form; head longer than broad; snout obtusely pointed; canthi distinct, lores concave; vome-

rine teeth in strong, oblique groups extending beyond level of choanae; a bony process at end of mandible; vocal sac openings present.

First finger longer than second; inner margins of second and third with narrow fold of skin. Toes with swollen tips having dorsal median groove; webbing as in typical form; fifth toe and metatarsal with wide, freely movable flap on outer edge.

Color (in alcohol) exactly like typical form.

Measurements (mm.): snout-vent 37.4; head length 15.7; head width 13.2; tympanum 3.0; tibia 21.0.

Paratype.—FMNH 121306, Samunsam valley, Sarawak. A female containing enlarged pigmented ova and agreeing with the holotype in all characters save those associated with sexual differences.

Snout-vent 53.4 mm.; tibia 31.3 mm.

Comparisons.—The presence of vocal sac openings and the enlargement of the mandibular processes prove that the holotype is sexually mature. Its size (37.4 mm.), therefore, can be taken as an adult dimension and is roughly half as large as that of *p. paramacrodon* (males 59.4–73.2). The female paratype is only slightly smaller than mature females of the nominate form. The tibia is 0.56–0.59 of snout-vent in the two specimens of *p. kenepaiensis*, 0.49–0.55 in 16 *p. paramacrodon.*

Rana paramacrodon kenepaiensis is like the Philippine forms compared to *p. paramacrodon* above in the possession of vocal sacs but is smaller than all of them except *leytensis.*

Range.—Western Borneo.

SARAWAK: First Division, Samunsam Valley. KALIMANTAN: Kenepai Mountains.

Rana signata signata Günther

Polypedates signatus Günther, 1872, Proc. Zool. Soc. London, **1872**, p. 600, pl. 40, fig. C—Matang, Sarawak.

Rana signata Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 71; 1920, Rec. Indian Mus., **20**, p. 177; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 226; Smith, 1925, Sarawak Mus. Jour., **3**, p. 32.

Rana signata signata Inger, 1954, Fieldiana, Zool., **33**, p. 312; 1956, *ibid.*, **34**, p. 407.

Rana obsoleta Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 147—Kina Balu, Sabah.

Rana picturata Boulenger, 1920, Rec. Indian Mus., **20**, p. 179—Borneo.

Material examined.—Borneo 164 (15 BM, including types of *picturata;* 121+larvae FMNH; 1 MHNP, type of *obsoleta*; 2 NSH;

1 RMNH; 21 SM; 3 ZMA); Malaya 7 (2 FMNH; 5 RM); Thailand 4 (MCZ).

Taxonomic notes.—Comparison of the types of *obsoleta* and *picturata* with topotypes of *signata* demonstrates that the first two are synonyms of *signata*.

Description.—A small *Rana*, males less than 50 mm., females less than 70 mm.; body moderate; legs short, slender; head triangular, obtusely pointed, width 0.30–0.35, length 0.35–0.38 of snout-vent; snout projecting, rounded in profile; nostril closer to tip of snout than to eye; eye large, subequal to snout; interorbital equal to or narrower than upper eyelid; lores weakly concave, vertical; canthi distinct; tympanum conspicuous, about one-half eye diameter; vomerine teeth in short oblique groups between choanae, distance between groups subequal to length of one group, groups farther from choanae.

Tips of fingers dilated into small disks having circummarginal grooves, all less than twice width of phalanges; disk of third finger less than half of tympanum diameter; first finger longer than second; fingers without fringes; supernumerary tubercles on three outer metacarpals. Disks of toes equal to those of fingers; web to bases of disks on outer sides of first three toes and on inner side of fifth, to distal subarticular tubercle of fourth toe or not so far, to distal subarticular tubercle on inner edge of third toe; outer metatarsals separated to bases; an oval inner and a strong, round outer metatarsal tubercle; tibia 0.48–0.57 of snout-vent.

Skin usually coarsely shagreened or granular above; no distinct dorsolateral fold; a weak supratympanic fold present or absent; ventral surfaces smooth; posterior portion of abdomen usually weakly rugose.

Color (in life) dark brown or black above with yellow or orange markings; a light line from tip of snout along canthus and edge of upper eyelid, and extending along dorsolateral area; dorsolateral light stripes usually interrupted, but complete to groin in about one-tenth of frogs; mid-dorsum with at least six rounded light spots but usually many more; in about one-tenth of sample light area of back more extensive than dark and forming a network; posterior face of thigh dark brown with light spots; dorsal surfaces of legs deep orange or yellowish brown with black cross-bars; ventral surface of body light gray to dark brown with small yellow spots.

In alcohol the orange and yellow fade to light grayish brown.

Secondary sex characters.—Females are larger than males. The snout-vent range in adult Bornean females is 48.4 (the smallest con-

taining enlarged, pigmented ova) to 68.7 mm.; the mean of 17 is 56.17 ± 1.51 mm. The snout-vent range of 58 Bornean males having nuptial pads is 33.2–46.8 mm. (mean $= 39.43 \pm 0.49$). Tympanum diameter, head length, and head width ratios do not show sex dimorphism. The ratio of tibia length to snout-vent is larger in males; the range in 20 males is 0.482–0.570 (median 0.523), in 15 females 0.480–0.560 (median 0.503). The difference between the two sets of ratios is statistically significant (Mann-Whitney $U = 78$; $P = 0.02$).

Males have paired subgular vocal sacs, nuptial pads on the median and dorsal surfaces of the first finger, and a humeral gland 2–3 mm. long (Boulenger, 1920; Inger, 1954A). Males also have a dorsal linea masculina.

Each granule on the backs of adult females is tipped with a central whitish asperity that is usually surrounded by a ring of smaller ones. These asperities give the skin of females a spinose appearance. Males are totally lacking in asperities either dorsally or ventrally. This species thus reverses the common dimorphism of other Malaysian *Rana*, e.g., *chalconota* and *nicobariensis*, in which the males bear asperities and the females are smooth.

Larvae.—Several lots of larvae (fig. 48) in stages of development from prior to hind limb bud to erupted fore limbs (Stage XX) were collected in Sabah and Sarawak. From Stage XVI onward an outer metatarsal tubercle is present. Stage XX larvae have circummarginal grooves on the weak disks of the digits, conspicuously barred hind limbs, light dorsal spots on a dark background, light spots forming an interrupted line on the canthus, and the webbing of adult *signata*. They also have white opaque glandules on the tail fins and on the sides of the head as in younger tadpoles (see below). The following description is based on 14 individuals.

Body oval, a little depressed, width about three-fourths length; eyes and nostrils dorsolateral; interorbital greater than internarial; nostril equidistant between eye and tip of snout; oral disk subterminal, width about half that of head; upper lip short; short, thick papillae in single row at lateral quarters of upper lip and continuous around lower one; labial teeth I:2+2/1+1:II and I:3+3/1+1:II with equal frequency; halves of divided upper rows widely separated; lower tooth rows subequal in length, innermost row very narrowly interrupted; beak weak, smooth edged, narrowly edged with black, upper broadly curved.

Spiracle sinistral, in a short tube, opening in line between eye and root of hind limb and midway between them; anus dextral, opening of tube at margin of ventral fin.

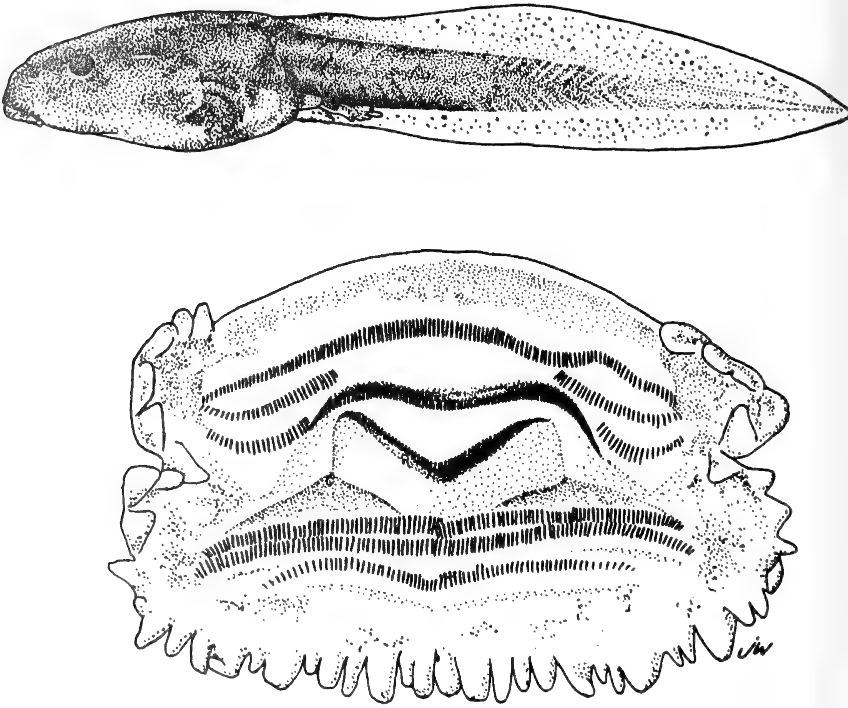


FIG. 48. Tadpole of *Rana signata* from Sabah.

Tail slender, scarcely deeper than body, tapering gradually in distal half; dorsal margin convex, ventral one straight, dorsal fin rising gradually from end of body, depth of fin slightly less than that of caudal muscle at point of maximum tail depth; ventral fin about two-thirds depth of dorsal.

Head, body, and fins covered with small whitish glandules; glandules concentrated in a wide dorsolateral band from eye to base of tail and connected with a ventrolateral band extending from hind limb forward to below spiracle; small clusters of glandules below and in front of eye and below and behind eye; a broad irregular band of glandules crossing head behind oral disk; a small isolated patch ventrally at rear of head.

Color (Stage XIV) of head and body dark brown above with a few small light spots, colorless below; caudal muscle and fins pale gray, uniform except for whitish glandules on fins; legs with dusting of fine melanophores dorsally.

Ecological notes.—*Rana signata* lives in and along small forest streams from one to ten meters wide. Seven out of 107 I collected were caught in old secondary growth; the remainder were caught in primary lowland rain forest. Sixteen were taken on low vegetation overhanging streams and the rest on the banks, from the water's edge to about one meter away. Calls were heard only at night. Very few Bornean specimens were caught farther than a few feet away from water, and they were all juveniles.

Larvae were collected in clear or slightly turbid waters, in shallow (less than 15 cm.) or deep (2 meters) water, and over silt or gravel bottoms.

All but two of the many Bornean specimens seen were caught at less than 600 meters above sea level. The highest known elevation for *signata* in Borneo is 1200 meters (Pa Ra near Bario, Sarawak). Mocquard (1890) recorded this species from "Kina Balu" without citing an elevation. As the large Kina Balu collection reported on by Smith (1931A) did not include *signata,* we may safely assume that it does not occur above 1000 meters there. Sumatran and Malayan localities are also in lowlands (Boulenger, 1912; van Kampen, 1923; Smith, 1930).

Breeding takes place in Borneo at least during the interval April-August and probably extends beyond that. Males were calling throughout that period and gravid females were obtained in May, June, and July. The only two adult females without enlarged ova were collected in June. Larvae were obtained in June and August. Except for three gravid females collected in November, I have no data on reproduction outside the April-August period.

Geographic variation.—As noted elsewhere (Inger, 1954A), the Bornean population of *signata* is more variable in coloration than the Philippine subspecies. Each Philippine subspecies seems to be characterized by a single type of pattern whereas all of the "Philippine" patterns occur in the Bornean form. The additional material examined since publication of the earlier paper confirms the difference in size between the Bornean form and the two neighboring Philippine subspecies, *signata grandocula* and *s. moellendorfi.*

The only geographic variation noted within the Bornean population is in the frequency of complete dorsolateral light stripes. Complete stripes were seen in four of 99 frogs from eastern Sabah and in 16 of 25 from Sarawak.

Range.—Peninsular Thailand, Malaya, Sumatra, and Borneo.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Kota Belud District, Kina Balu (Mocquard, 1890); Sandakan District, Sandakan, Sapagaya Forest Reserve; Tawau District, Kalabakan. SARAWAK: First Division, Bidi, Matang, Mount Penrissen, Samunsam valley; Second Division, Lupar River valley; Third Division, Baleh River near mouth of Putai River; Fourth Division, Akah River, Niah, Pa Ra near Bario, Tutoh River valley; Fifth Division, Lawas. KALIMANTAN: Barabei, Semberrah.

Ooeidozyga

KEY TO BORNEAN FORMS OF OOEIDOZYGA.

Fourth toe broadly webbed to disk on both sides; chest and abdomen whitish, without spots . . . . *O. laevis*

Fourth toe not webbed to disk on both sides; chest and abdomen spotted *O. baluensis*

Ooeidozyga baluensis may be confused in the field with *Rana microdisca finchi*, which shares its habitat. The lower lip of *R. m. finchi* has conspicuous dark bars, that of *O. baluensis* does not.

Ooeidozyga baluensis (Boulenger)

Oreobatrachus baluensis Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 401, pl. 17—Kina Balu, Sabah; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 229

Ooeidozyga baluensis Inger, 1956, Fieldiana, Zool., **34**, p. 401.

Phrynoglossus baluensis Smith, 1931, Bull. Raffles Mus., no. 5, p. 15.

Material examined.—Borneo 161 (1 AMNH; 155 FMNH; 3 UMMZ; 2 USNM).

Description.—A small ranid, adults less than 35 mm.; habitus stocky; head width 0.29–0.37 of snout-vent; snout rounded, projecting, equal to or slightly larger than eye diameter; nostrils oriented laterally; canthus rounded, lores oblique; tympanum present, partly obscured by skin, one-half to three-fifths eye diameter; interorbital narrower than upper eyelid; no vomerine teeth; tongue oblong, usually emarginate.

Fingers bluntly rounded; first equal to or shorter than second; toes with distinct disks lacking circummarginal grooves; first two toes broadly webbed to disks on outer edges; third and fifth toes webbed to disks or with one phalanx free of broad web, fourth with two to three phalanges free of broad web on outer side; subarticular tubercles weak; oval inner metatarsal tubercle one-half length of first toe;

usually a small outer metatarsal tubercle; tibia 0.46–0.57 of snout-vent.

Skin of back with irregular glandular ridges; usually a dorsolateral ridge behind eye and an inverted U-shaped one between shoulders; numerous small, round warts on sides; abdomen rugose; throat with low warts; a supratympanic fold from eye to axilla.

Color (in life) dark brown, fading to tan in sacral region; sides and dorsal surfaces of limbs tan; limbs with black crossbars; ventrally white, with black and brown spots.

Secondary sex characters.—Only one female (33.3 mm.) contained enlarged ova. A second female measured 34.0 mm. Smaller females (up to 27.1 mm.) had slender, non-convoluted oviducts and were evidently immature. Adult males (with vocal sacs and nuptial pads) measured 16.0–26.2 mm. (mean 21.65 ± 1.26; $N = 8$).

The vocal sacs, which have round openings near the commissures of the jaws, are paired and sublingual. The yellowish nuptial pad covers the dorsal and medial surfaces of the first finger from its base to the beginning of the terminal phalanx. The largest male (26.2 mm.) had colorless asperities on the chin and throat. Males also have pinkish lineae masculinae at the dorsal and ventral edges of the oblique muscle.

Ecological notes.—Specimens from northeastern Borneo were caught in poorly drained, lowland rain forest, half of them on the banks of small streams and the remainder on the forest floor. This species is not confined to flat, forested areas, as we have taken large numbers in very rough primary hill forest in Sarawak. Even here, however, it is most abundant in small, flat seepage areas in narrow valleys. A few were caught in association with *Rana laticeps* in tiny streams trickling slowly over rocks.

Previously reported specimens were collected mainly on Mount Kina Balu 900–1370 m. above sea level. All the Sarawak frogs (137) and those from eastern Sabah (14) were caught within 350 m. of sea level.

Geographic variation.—Sarawak specimens have more extensive webbing than do those from northern Borneo. Generally the third and fifth toes are broadly webbed to the disks in frogs from Sarawak but have one or two phalanges free in those from Sabah. The fourth toe shows parallel variation.

Range.—Borneo.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Kota Belud District, Bundu Tuhan, Kenokok, Kiau; Sandakan District, Sepilok Forest Reserve. SARAWAK: First Division, Matang; Third Division, Nanga Tekalit; Fourth Division, Labang, Sungei Pesu. KALIMANTAN: Njapa, Sungei Berau.

Ooeidozyga laevis laevis (Günther)

Oxyglossus laevis Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 7, pl.1 , fig. A—Philippine Isands; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 230, fig. 26; Smith, 1925, Jour. Sarawak Mus., **3**, p. 33.

Ooeidozyga laevis Smith, 1927, Proc. Zool. Soc. London, **1927**, p. 204.

Ooeidozyga laevis laevis Inger, 1954, Fieldiana, Zool., **33**, p. 249; *ibid.*, **34**, p. 400.

Phrynoglossus laevis Smith, 1931, Bull. Raffles Mus., no. 5, p. 16.

Material examined.—Borneo 166 (156 FMNH; 1 NSH; 1 RMNH; 8 SM); Sumatra 1 (ZMB); Philippine Islands 165 (FMNH); Singapore 3 (FMNH); Malaya 4 (BM); Thailand 2 (1 FMNH; 1 ZMB); Burma 6 (ZMA).

Taxonomic notes.—The form *laevis martensi* (Peters) (type locality Bangkok) differs from the typical subspecies in having smaller toe disks (Smith, 1922), a larger inner metatarsal tubercle, and less extensive webbing. The disk of the fifth toe in *laevis laevis* is scarcely wider than the penultimate phalanx and is about one-half the widths of the disks on the other toes. In *laevis martensi* all of the disks are the size of the fifth one in *l. laevis*. The inner metatarsal tubercle is more strongly compressed in *martensi* and its length goes into that of the first toe 1⅓–1½ times. In *l. laevis* the tubercle is less strongly compressed and its length goes into that of the toe at least two times. Though the web reaches the disks of all of the toes in *martensi*, it is deeply excised and the membrane midway between the two outer toes does not reach the level of the center subarticular tubercle of the fourth toe. In *l. laevis* the corresponding point lies distal to that tubercle.

Frogs from Perak and Singapore agree with those from Borneo and the Philippine Islands (*laevis laevis*) in the above characters. Those from Burma and northwestern Thailand are like those from Bangkok (*l. martensi*).

Description.—A small ranid, males 20–30 mm., females 25–45 mm.; habitus stocky; limbs short, heavy; head depressed, tapering to rounded snout; nostrils oriented dorsally or dorsolaterally; canthus broadly rounded or not distinct; lores sloping; tympanum present, not visible through skin; no vomerine teeth; tongue oval, rear margin entire or very feebly notched.

Fingers without disks or fringes of skin; first finger equal to or longer than second. Toes with disks, that of fifth toe scarcely wider than phalanges and half width of other disks; web reaching disks of all toes, not emarginate; a ridge of skin on outer edge of fifth toe; inner metatarsal tubercle compressed, less than half length of first toe; outer metatarsal tubercle minute, usually absent; tibia 0.41–0.51 of snout-vent.

Skin of back smooth anteriorly, with small, white, spinules posteriorly; similar spinules on dorsal and lateral aspects of hind limbs; round or oval warts on sides; throat various (see *Secondary sex characters*); abdomen rugose; a weak supratympanic fold from eye to axilla.

Color (in alcohol) gray or brown above with obscure darker markings; a few individuals with a light vertebral line; ventral surfaces cream-colored; throat immaculate, with small dark spots, or, rarely, dark brown; abdomen immaculate or with a few small spots; ventral surfaces of hind limbs usually with small spots; rear surface of tarsus black, contrasting with lighter dorsal surface.

Secondary sex characters.—Females from Sabah having enlarged, convoluted oviducts measure 34.6–45.7 mm., snout to vent (mean 38.39 ± 1.00 mm.; $N = 13$). Five adult males from the same area measure 20.6–31.4 mm. (mean 26.9 mm.). Two adult females from Sarawak measure 26.6 and 27.1 mm., whereas one adult male is 21.9 mm. long. Similar differences between the sexes are seen in Philippine samples (Inger, 1954A).

Males have a colorless linea masculina at the dorsal border of the obliquus muscle and, as noted elsewhere (*ibid.*), median subgular vocal sacs, whitish spinules in the gular regions, and nuptial pads on the first fingers. Occasional males having the other sex characters lack the gular asperities.

Larvae.—No tadpoles have been recorded from Borneo yet. Larvae reported from other parts of the range have low caudal fins, a terminal mouth, no labial teeth or papillae, and the lower lip horseshoe-shaped (Smith, 1916A; van Kampen, 1923). Metamorphosis takes place while the animals are small; frogs 12.0–14.9 mm. long had traces of a tail.

Ecological notes.—In Borneo *laevis* is found in or near small streams or isolated pools in forest or clearings. Twenty-nine frogs were caught in or along streams and 35 in or near pools. The last may be small holes in a trail, such as are left by elephants in soft earth, or ruts in a road, or rain-filled pig wallows in forest. Thirty-eight were caught

in flat, swampy, primary forest, seven in better drained forest, seven in secondary growth or rubber plantations, and 13 in large clearings. In the clearings they occurred with *Rana nicobariensis* and *Rhacophorus macrotis*. Along small forest streams *laevis* was found with *Rana blythi* and young *Leptobrachium hasselti*.

All Bornean *laevis* examined by me were collected within 350 meters of sea level. Smith (1925B) reported *laevis* from 1200 meters on Mount Dulit. In the Philippines it ranges from sea level to 1070 meters (Inger, 1954A), and on Bali it is abundant between 500 and 1000 meters (Mertens, 1930). Van Kampen (1923) listed Celebesian localities lying between 500 and 1100 meters, but some of his specimens may belong to the species subsequently described by Smith (1927) from the mountains of Celebes.

TABLE 31.—Comparison of samples of adult females of *Ooeidozyga laevis laevis*.

	Sarawak	Malaya	Eastern Sabah	Negros	Mindanao
			Snout-vent length (mm.)		
Range	25.8–28.7	29.2–33.2	34.6–45.7	32.7–52.6	37.2–60.8
No.	4	5	13	25	14
Mean	27.05	31.72±0.71	38.39±1.00	43.02±1.11	44.85±1.92
		Analysis of variance: $F(4, 55)=10.465$; $P<0.01$			
			Tibia/snout-vent (in thousandths)		
Range	441–505	—	414–497	414–454	371–447
No.	4		14	16	14
Median	482		456	432	412
		Kruskal-Wallis analysis of variance: $H=24.816$; $P<0.001$			

Geographic variation.—In addition to the differences between subspecies discussed under *Taxonomic notes*, this species shows local variation within subspecies. Sarawak specimens are near in size to those from Malaya but smaller than frogs from eastern Sabah, which in turn are smaller than those from Mindanao and Negros (Table 31). Males were omitted from the comparison as so few were at hand. The samples also differ in the ratio of tibia to snout-vent. Though the differences in tibia ratios of Table 31 seem to be related to changes in snout-vent, grouping specimens by size classes shows that snout-vent differences cannot explain the tibia differences. The median tibia ratios for females in the 36.0–39.9 mm. class are: Sabah 456, Negros 437, and Mindanao 413. In the 40.0–44.9 mm. class, the three medians are, respectively, 422, 435, and 410.

Range.—From the Malay Peninsula (south of the Isthmus of Kra) to Flores (Mertens, 1930), Celebes (van Kampen, 1923), and Luzon.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Lahad Datu District, Lahad Datu; Sandakan District, Sandakan, Sapagaya Forest Reserve, Sepilok Forest Reserve; Tawau District, Kalabakan; Tuaran District, Tuaran. SARAWAK: First Division, Kuching, Matang, Tanjong Paoh; Third Division, Mengiong River, Mount Dulit (Smith, 1925B); Fourth Division, Baram (van Kampen, 1923), Labang, Niah. KALIMANTAN: Sebruang (*ibid.*), Sungei Siniai.

Staurois Cope

The genus *Staurois* Cope (type species *Ixalus natator* Günther—by original designation[1]) was redefined by Boulenger (1918) as a group of ranids having digital disks broader than long, T-shaped terminal phalanges, no intercalary bone or cartilage, outer metatarsals separated to the base by web, small nasals separated from each other and from frontoparietals, and omosternal style not forked. All of these characters are shared by *Simomantis* Boulenger, which differs from that definition of *Staurois* only in possession of web between the outer fingers, as Boulenger (1918) himself observed. On the basis of the adults, the genus *Simomantis* cannot be maintained as distinct from *Staurois*. I therefore recommend that *Simomantis* Boulenger be placed in the synonymy of *Staurois* Cope.

Staurois has been retained as a valid taxon by Noble (1931) and Liu (1950) solely on the basis of a torrent-adapted tadpole having a distinctive abdominal sucker. But the larva of the type species has been unknown (Inger, 1954A). In fact, no ranid tadpole having a suctorial ventral disk has been reported from the Philippine Islands where *natator* is locally very abundant.

A field party of Field Museum of Natural History obtained 215 adult *S. natator* on Mounts Apo and McKinley, Mindanao, but no larvae. The proper habitat for specialized rhyacophilous tadpoles was searched as the party collected 86 adult and 20 torrent-adapted larvae of *Ansonia muelleri* at the same time and place.

Specialized torrent-dwelling tadpoles of the type described by Noble (1931) and Liu (1950) are known from Borneo (see p. 270 ff.).

[1] Cope (1865) listed three species: *Ixalus natator*, *I. guttatus*, and *Hyperolius plicatus* all of Günther. The last is a *Phrynobatrachus*. *Ixalus guttatus* is a synonym of *natator*.

None of those that can be assigned to known species of adults can be identified with any of the Bornean species of *Staurois* recognized by Boulenger (1918), including *natator*. Reasons for doubting the assignment of Mocquard's (1890) larvae to *Ixalus nubilus* Mocquard (=*S. natator*) are given elsewhere (Inger, 1954A).

Three specialized ranid larvae have been collected in Mindanao, two (FMNH 50954) on Mt. McKinley where adults of *S. natator* were caught and one (SU 3872) on Mt. Dapitan where a field party under A. Alcala obtained adults and young of *S. natator*. These larvae, described in greater detail below, have deep cup-like lips but no abdominal sucker. Their upper lip has two continuous rows of papillae and their lower lips a broad, continuous band of papillae. The beaks are moderate in thickness and smooth except for serrate edges. Their limbs have not developed far enough to provide evidence of identity. However, the association with habitats of adult *S. natator* and the absence of tadpoles having abdominal suckers from the Philippine Islands lead me to conclude that these are, in fact, the larvae of *natator*.

Similar larvae (FMNH 77523–4, 130918–20) ranging in development from earliest limb-bud stages to Stage XVIII, have been found in Borneo. The more advanced of these Bornean tadpoles (fig. 49) have webbing between the fingers. The only Bornean ranid having this feature is *Simomantis latopalmata*, which as noted above has every diagnostic character of *Staurois* listed by Boulenger (1918). Thus the Philippine tadpoles resemble Bornean ones that are clearly those of *Simomantis*, adults of which are congeneric with *Staurois natator*.

A juvenile *Staurois natator* (SU 20018), collected in the same general vicinity as the Dapitan tadpole (SU 3872), was, when caught, in the process of resorbing the tail (4.5 mm., equal to 0.34 of snout-vent). It has opercular "scars" at the axillae and the gape of the mouth reaches a perpendicular from the center of the eye. Certain Bornean larvae (FMNH 136327, 137865) in comparable stage of limb development—i.e., fore limbs erupted, opercular scars present, tail partly resorbed (0.13–0.37 of snout-vent)—still retain complete abdominal suckers of the type characteristic of tadpoles assigned mistakenly, I believe, by Noble to the genus *Staurois*. In the most advanced of these Bornean larvae (137865), the tail is only 1.7 mm. long and the gape of the mouth reaches a perpendicular from the front of the eye. These Bornean tadpoles demonstrate that those having abdominal suckers retain this structure in the stage of development reached by the metamorphosing Philippine *Staurois* (SU 20018). This line of

evidence also supports the ideas that the larva of *Staurois natator* does not have an abdominal sucker and that the Mindanao larvae are properly assigned to that species.

If the tadpole of *S. natator* has been correctly identified, the genus *Staurois* can be retained on the same basis as before, i.e., on the basis of a peculiar specialized larva, but the definition must be changed radically from that used by Noble (1931) and Liu (1950). The larvae here assigned to *Staurois* live in swift streams having rock and gravel bottoms. Although I have not actually observed them alive, those I have collected were obtained by poison in shallow, swift water where the tadpoles could have maintained themselves by wiggling among the rocks of the bottom and clinging to them with their deep cup-like lips. These tadpoles evidently do not cling to exposed rock surfaces, as do larvae of the type having abdominal suckers. Their cryptic habits may explain why so few *natator* larvae have been collected in the Philippine Islands.

Provisionally, I include in the genus *Staurois* only those species listed by Boulenger (1918, p. 374) as *Staurois*, excluding *larutensis* Boulenger which has a tadpole equipped with an abdominal sucker, but including the species formerly known as *Simomantis latopalmata*.

Those riparian ranids having rhyacophilous larvae provided with abdominal suckers belong in a different genus for which the name *Amolops* Cope is available (see p. 256).

The three Bornean species assigned to the genus *Staurois* in this publication may be distinguished on the basis of the following key.

1A. Outer fingers webbed .... *S. latopalmatus*.
1B. Fingers not webbed .... 2.

2A. Outer metatarsal tubercle present; no lingual papilla .... *S. natator*.
2B. No outer metatarsal tubercle; lingual papilla present .... *S. tuberilinguis*.

Staurois natator Günther

Ixalus natator Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 75, pl. 4, fig. C—Philippines

Staurois natator Cope, 1865, Nat. Hist. Rev., **1865**, p. 117; Inger, 1954, Fieldiana, Zool., **33**, p. 335, fig. 59.

Ixalus guttatus Günther, *op. cit.*, p. 76, pl. 4, fig. D.—Borneo.

Staurois guttatus Boulenger, 1918, Ann. Mag. Nat. Hist., (9), **1**, p. 374; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 235; Smith, 1925, Sarawak Mus. Jour., **3**, p. 33.

Rana guttatus Smith, 1931, Bull. Raffles Mus., no. 5, p. 30.

Rana natatrix Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 71.

Ixalus nubilus Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **2**, p. 153, pl. 11, fig. 3—Palawan.

Staurois nubilus Boulenger, 1918, *op. cit.*; van Kampen, *op. cit.*, p. 236.

Material examined.—Borneo 49 (9 BM, including type of *guttatus;* 16 FMNH; 19 NSH; 1 RMNH; 4 UMMZ); Palawan 45 (20 FMNH; 10 MCZ; 5 UMMZ; 10 USNM); Mindanao 235 (FMNH); Leyte 16 (FMNH).

Taxonomic notes.—Taylor's opinion (1920) that *nubilis* is a synonym of *natator* is confirmed by examination of additional Palawan material. A feebly developed lingual papilla appears in some individuals that do not otherwise differ from frogs lacking the papilla.

The Bornean population (*guttatus*) was thought to differ from Philippine *natator* by the presence of vomerine teeth (Boulenger, 1894A; Inger, 1954A). Only half of the Bornean frogs seen have vomerine teeth on both sides of the mouth; the remainder have vomerine teeth on only one side or (in one specimen) none at all.

One character does distinguish the Bornean sample from the Philippine. The ova of Bornean females once they grow to 1.0 mm. are entirely black; ova that size in females from Palawan, Mindanao, and Leyte are yellowish or orange. These observations were made on specimens collected at various times and by various collectors so that the difference cannot be attributed to differences in preservation or time of collection. Boulenger (1918) also noted this difference between Bornean and Philippine females. It is possible, judging by what is known of the inheritance of melanic pigmentation in mice and guinea pigs (reviewed in Haldane, 1954), that this striking difference reflects a single gene difference between populations. The ecological significance can only be guessed at in the absence of observations. Pigmented ova are usually laid in places exposed to light, non-pigmented ones in places protected from light (e.g., under stones, in tree holes, etc.). Thus the difference in pigmentation suggests a difference in site of oviposition that is yet to be confirmed.

As will be shown below (*Geographic variation*) the regions of change of a number of characters do not coincide. At the present only the arbitrary (and hence inadvisable) selection of a single character as a guide would permit the naming of forms.

Description.—A moderate-sized frog, 30–55 mm.; body and limbs slender; head length 0.33–0.39 of snout-vent, width 0.26–0.29; snout narrow, rounded, projecting slightly; nostril twice as far from eye as from tip of snout; canthus acute, curved; lores deeply concave,

oblique or vertical; interorbital narrower than upper eyelid; eye large, equal to snout or to eye-nostril distance; tympanum distinct, one-third to one-half eye diameter; vomerine teeth present on both sides or on one side only; no lingual papilla.

Fingers with large disks having circummarginal grooves; disks of two outer fingers wider than tympanum; first finger shorter than second; second and third fingers with fringes of skin; no supernumerary metacarpal tubercles. Disks of toes narrower than those of two outer fingers; all toes webbed to disks; an oval inner and a smaller, round outer metatarsal tubercle; tibia 0.55–0.65 of snout-vent.

Skin above and on sides coarsely granular; no supratympanic fold; several large, flat glands at rictus and above axilla; throat smooth; skin rugose on chest becoming granular posteriorly.

Color (in alcohol) brown above with numerous large black spots; a narrow black stripe from tip of snout to eye just below canthus; side of body and head below loreal stripe white or ivory; dorsal surfaces of limbs with dark crossbars; ventral surfaces white, immaculate. In life ventral surfaces greenish.

Secondary sex characters.—Bornean females with enlarged and convoluted oviducts measure 44.1–54.6 mm. (mean 49.69 ± 0.75; $N = 18$); the smallest with apparently mature ova (1.6–1.9 mm.) measures 45.3 mm. Bornean males with vocal sacs measure 29.4–36.2 mm. (mean 33.24 ± 0.40; $N = 18$). As in the case of Philippine frogs (Inger, 1954A), Bornean males have wider tympana: males 0.056–0.071 ($N = 4$), females 0.041–0.052 ($N = 7$). However, unlike the Philippine sample, Bornean frogs show no sexual dimorphism in head width or tibia length.

The yellowish nuptial pad covers the entire dorsal and median surfaces of the first finger from its base to the end of the metacarpal. The paired subgular vocal sacs open near the commissures of the jaws. The males lack lineae masculinae.

Larvae.—The following description is based on the three tadpoles from Mindanao (FMNH 50954, SU 3872) mentioned above (p. 244). They are in hind limb Stages II to XIII.

Body oblong, slightly depressed, width about three-fifths length; snout broadly rounded; eyes and nostrils dorsolateral; interorbital three-fourths length of snout, $1\frac{1}{2}$ times eye-nostril distance, wider than internarial; nostril closer to eye than to end of snout; spiracle sinistral, low on side, tube about half diameter of eye, opening closer to eye than to end of body; anal tube dextral; head and body without patches of glands; no abdominal disk.

Oral disk ventral; lips large; papillae in two to four rows on upper lip, in four to six rows on lower lip; labial teeth I:2–2 or II:2–2 on upper lip, 1–1:II or III on lower lip, those of outermost rows on both lips weakest, those of inner row on lower lip strongest; rows subequal in lateral extent; beaks strong, black, angulate but not M-shaped, edges coarsely serrated.

Tail lanceolate, broadly rounded at tip; caudal muscle deeper than either fin except near tip; margins of fins weakly convex; dorsal fin deeper than ventral.

Head and body dark brown above, with faint light spots; caudal muscle and dorsal fin with large dark spots; ventral fin colorless.

Head plus body 7.5 (Stage II), 9.1 (Stage VI), and 9.5 mm. (Stage XIII).

Ecological notes.—Bornean frogs were collected on large rocks at the edges of swift, clear streams in rain forest, agreeing with observations on Philippine frogs (Taylor, 1920; Inger, 1954A). At Matang, Sarawak, *natator* was much more conspicuous by day than other species (e.g., *Amolops jerboa* and *Rana kuhli*) occupying the same habitat.

Although strictly comparable data are not available, *S. natator* appears to be more abundant in the Philippines than in Borneo. On Mount Apo, Mindanao, the Philippine Zoological Expedition collected more *Staurois natator* (191) than any other ranid, 17 of them in one day along a creek (Hoogstraal, 1951, p. 48) very similar to Sungei China at Matang. Only nine *natator* were caught in four days at Matang in contrast to 72 *Amolops jerboa,* which sits on the same spray-moistened rocks and appears to have habits similar to those of *natator*. On Mount Apo no other ranid has habits like those of *natator*, and it may be that lack of competition permits the development of larger populations in the Philippines.

In Borneo *natator* has been collected between 150 and 1300 meters (van Kampen, 1923), with most of the known localities lying below 1000 meters.

Females collected in April (two out of three) and August (five out of seven) in Sarawak contained enlarged ova. Males from the same collections had well-developed nuptial pads.

Geographic variation.—Variation in vomerine teeth and in the pigmentation of enlarged ova has been described above (p. 246).

Bornean and Palawan frogs have black spots in a light background, whereas frogs from other Philippine Islands have light spots in a dark background or are uniformly dark (Inger, 1954A). In the

Table 32.—Geographic variation of *Staurois natator* in size and body proportions (given in terms of thousandths of snout-vent).

	Males			Females		
	Borneo	Palawan	Mindanao	Borneo	Palawan	Mindanao
Snout-vent (mm.)						
No.	18	12	25	18	16	24
Range	29.4–36.2	29.4–33.3	29.8–43.7	44.1–54.6	39.5–46.6	41.0–50.2
Mean	33.24±0.40	31.20±0.39	40.32±0.56	49.69±0.75	42.55±0.56	45.12±0.44
Head width/snout-vent						
No.	11	11	25	9	15	23
Range	261–292	299–336	265–308	256–288	280–334	255–289
Median	274	316	283	272	299	272
		H*=27.96;	P<0.001		H*=26.65;	P<0.001
Tympanum/snout-vent						
No.	4	11	25	7	13	23
Range	56–71	44–65	31–52	41–52	38–51	28–48
Median	62	53	44	49	43	37
		H*=20.08;	P<0.001		H*=14.88;	P<0.001
Tibia/snout-vent						
No.	9	12	24	15	16	23
Range	589–645	557–631	560–632	549–634	527–620	532–596
Median	607	591	597	593	558	562
		H*=2.69;	P>0.2		H*=8.72;	P=0.02

* Calculated from Kruskal-Wallis analysis of variance (Siegel, 1956).

samples at hand, males from Borneo and Palawan were approximately equal in size and smaller than those from Mindanao, whereas females from Borneo were larger than those from the other two islands (Table 32). In relative head width, Bornean and Mindanao frogs were similar, but smaller than those from Palawan (Table 32). The three samples differed significantly from one another in tympanum diameter, the Palawan sample being intermediate. Males of the three samples did not differ in tibia length; females from Palawan and Mindanao had similar leg lengths and differed from Bornean females (Table 32).

Considering the variation described above, two features are outstanding. One is the independent variation of characters, which leads to the second feature, namely uncertain coincidence in zones of change. The change in pigmentation of the ova (Borneo *vs.* the others) coincides with the differences in vomerine teeth. But the vomerine teeth show incomplete development in the only population in which they appear. Size differences of females coincide with differences in ova; in this case, however, the females show one pattern and the males another. The most logical interpretation of these observations is that we do not have a dichotomy between Bornean and non-Bornean populations, but rather three independently diverging groups. The latter situation is an expected consequence of the three-way isolation—Palawan-Borneo-Mindanao—that has existed since the end of the Pleistocene.

Range.—Western and northern Borneo to the Calamianes in the western Philippine Islands and to Leyte and Samar in the eastern Philippine Islands.

SABAH: Kota Belud District, Mount Kina Balu; Ranau District, Sungei Kepungit, Sungei Mamut; Tambunan District, Sungei Kaingeran. SARAWAK: First Division, Mount Gadin (Smith, 1925B), Lundu, Matang, Mount Penrissen (*ibid.*), Samunsam valley; Second Division, Lupar River valley; Third Division, headwaters of Baleh River, Mount Dulit (van Kampen, 1923), Mengiong River; Fourth Division, Lejok, Sungei Melana, Meligong, Sungei Patah, Long Sinei; Fifth Division, Lawas. KALIMANTAN: Sebruang (*ibid.*), Mount Simedum near Sambas.

Staurois tuberilinguis Boulenger

Staurois tuberilinguis Boulenger, 1918, Ann. Mag. Nat. Hist., (9), **1**, p. 374, Mount Kina Balu, Sabah; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 237; Smith, 1925, Sarawak Mus. Jour., **3**. p. 33.

Rana tuberilinguis Smith, 1931, Bull. Raffles Mus., no. 5, p. 17.

Staurois parvus Inger and Haile, 1960, Sarawak Mus. Jour., **9**, p. 273, figs. 3–4—Meligong, Akah River, Sarawak.

Material examined.—Borneo 14 (7 BM, including holotype of *tuberlinguis;* 3 FMNH, including holotype of *parvus;* 3 NMB; 1 SM, paratype of *parvus*).

Taxonomic notes.—Both Boulenger (1918) and van Kampen (1923) were mistaken in stating that the first finger of *tuberilinguis* was longer than the second. The first finger is much shorter than the second in all specimens including the holotype. This error in the literature indirectly led to the mistaken idea that *parvus* represented a distinct species. The paratype of *parvus* is much smaller (29.0 mm.) than the holotype of *tuberilinguis* (43.4 mm.), yet both are mature females containing enlarged ova. Other females (31–38 mm.) bridge the gap.

Description.—A small frog, 20–40 mm.; body and limbs slender; head length 0.32–0.39 of snout-vent, width 0.26–0.30; snout obtusely pointed or truncate, sloping downward and backward to mouth in profile; nostril slightly closer to tip of snout than to eye; canthus acute, curved; lores concave, oblique; interorbital subequal to upper eyelid; eye large, subequal to snout; tympanum visible, one-third to two-fifths eye diameter; no vomerine teeth; prominent lingual papilla present.

Fingers with large disks having circummarginal grooves, disks of two outer fingers much wider than tympanum; first finger shorter than second; fingers without lateral fringes of skin; no supernumerary metacarpal tubercles. Disks of toes narrower than those of outer fingers; all toes webbed to disks; an oval inner metatarsal tubercle; a small outer metatarsal tubercle present in about one-third of individuals; tibia 0.49–0.57 of snout-vent.

Skin above coarsely granular, with low, oval warts in some specimens; sides with low, oval glands; abdomen smooth or weakly rugose.

Color (in alcohol) black or brown above, with obscure lighter markings; limbs with dark crossbars dorsally; below white or cream-colored, usually with dark spots on throat and chest.

Secondary sex characters.—Seven females containing enlarged, non-pigmented ova measure 29.0–43.4 mm. (mean 35.83 ± 1.76); two males with vocal sacs measure 22.1 and 22.9 mm. The oviducts have networks of melanophores.

The vocal sacs are paired and sublingual. A whitish nuptial pad covers the dorsal and median surface of the first metacarpal.

Ecological notes.—This species has been collected in primary rain forest and old secondary growth, and at elevations between 100 and 1700 meters. Most of the known specimens were caught at 900 meters (Smith, 1931A).

Range.—Western Sabah and Sarawak.

SABAH: Kota Belud District, Kenokok (Smith, 1931A), Kiau, and Lumu Lumu on Mount Kina Balu; Ranau District, Sungei Kepungit, Sungei Liwagu, Sungei Mamut, Sungei Matukungan. SARAWAK: First Division, Mount Penrissen (Smith, 1925B); Fourth Division, Bario, Lejok River, Mount Batu Song (Boulenger, 1918), Meligong River.

Staurois latopalmatus (Boulenger)

Ixalus latopalmatus Boulenger, 1887, Ann. Mag. Nat. Hist., (5), **20**, p. 97—Mount Kina Balu, Sabah.

Simomantis latopalmata Boulenger, 1918, *ibid.*, (9), **1**, p. 373; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 238; Smith, 1931, Bull. Raffles Mus., no. 5, p. 17.

Material.—Borneo 55+10 series of larvae (1 AMNH; 7 BM; 22+9 series of larvae FMNH; 1 NHMW; 2 RMNH; 21+larvae SM; 1 ZMB).

Description.—A moderate-sized frog, males 40–50 mm., females to 65 mm.; body stocky; limbs long but heavy; head length 0.30–0.36 of snout-vent, width 0.31–0.36; snout almost truncate, sloping downward and backward to mouth in profile, snout much shorter than diameter of eye; nostril closer to end of snout than to eye; canthus acute, curved; lores concave, sloping; interorbital narrower than upper eyelid; eye large; tympanum visible, one-third to two-fifths diameter of eye; no vomerine teeth; no lingual papilla.

Fingers with large disks having circummarginal grooves, disks of all fingers wider than tympanum; first finger shorter than second; web between second and third fingers usually reaching subarticular tubercle of second, to disk of third as a fringe; web between third and fourth fingers to distal subarticular tubercles of both fingers or beyond; no supernumerary metacarpal tubercles. Disks of toes narrower than those of fingers; fifth toe only slightly shorter than fourth; all toes fully webbed to disks; a narrow fringe on inner edge of first and on outer edge of fifth toe; a low, oval inner metatarsal tubercle; no outer metatarsal tubercle; tibia 0.58–0.71 of snout-vent.

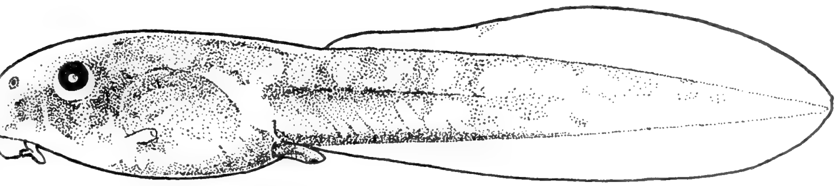
Skin above rugose or coarsely granular; no supratympanic fold; abdomen smooth or weakly rugose posteriorly.

Color (in life) black above with small, scattered, yellow spots; dorsal surfaces of limbs with narrow crossbars formed of rows of small yellow spots; ventral surfaces ivory, immaculate.

Secondary sex characters.—Five adult females measure 57.8–63.4 mm. (mean 61.38); the smallest contains enlarged ova. Sixteen males with vocal sacs measure 39.6–49.3 mm. (mean 45.26 ± 0.63).

The vocal sacs are paired, sublingual, and widely separated. Each sac bulges out forcing the lateral gular skin to form a permanent pouch. The whitish nuptial pad covers the dorsal and medial surfaces of the first metacarpal.

Larvae.—Ten series of tadpoles (Stages I to XVIII) are assigned to this species (fig. 49). The position of the vent is distinctly ranid



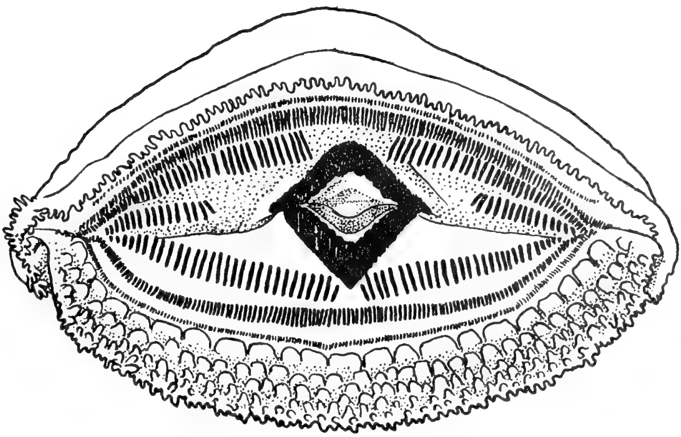


FIG. 49. Tadpole of *Staurois latopalmatus* from Sarawak.

(in the restricted sense) and the more advanced larvae (Stages XVII–XVIII) have the fore limb developed far enough to see the diagnostic webbing between the fingers.

Body oblong, slightly depressed, width about one-half length; snout broadly rounded; eyes and nostrils dorsolateral; interorbital two-thirds eye-snout distance, longer than eye-nostril; nostril closer to eye than to end of snout; spiracle sinistral, low on side, tube two-thirds eye diameter, opening midway between eye and end of body; anal tube dextral, separate from remainder of ventral fin beyond Stage XI; head and body without patches of glands; no spinules; no abdominal disk.

Oral disk ventral; lips long, forming a deep cup (fig. 49); papillae in three or four rows around both lips; teeth II:2–2/1–1:II to II:2-2/V (see *Geographic variation*), those of outer row on both lips weak, those of inner rows much the strongest; rows subequal in lateral extent; beaks strong, angulate, not M-shaped, black, coarsely serrated.

Tail lanceolate, broadly rounded at tip; upper fin equal to caudal muscle in distal half, margin convex; ventral fin not as deep as upper, margin almost straight.

Color (in alcohol) of head and body uniform brown above, colorless below; caudal muscle with dusting of melanophores, usually clustered into a few large spots; upper fin with a few indistinct spots; lower fin colorless or with one or two spots near tip.

Head-plus-body lengths vary from 5.9 (Stage III) to 13.5 mm. (Stage XVII); tail 0.59–0.67 of total length.

Ecological notes.—All 26 adults and subadults for which detailed information is available were caught on boulders or on gorge walls of swift, clear streams flowing through primary forest or secondary growth. When disturbed these frogs skitter over the surface of the water, no matter how swift, to another rock. Larvae were collected in the same type of stream, though direct observations were not made on them.

This species has a wide altitudinal range, but more specimens have been caught at low elevations. Of the adults seen, 28 were caught within 200 meters of sea level, 16 between 200 and 300 meters, eight between 450 and 600 meters, and three at 1000 meters above sea level.

Geographic variation.—The number of labial tooth rows is higher in larvae from the eastern slopes of Mount Kina Balu (Ranau Dis-

trict) than in those from the Third and Fourth Divisions, Sarawak. The tooth counts on the lower lips in the Sarawak tadpoles are 1–1:II (11 specimens) and III (1); in the Sabah tadpoles 1–1:III (2), IV (2), and V (4). As the Sarawak sample includes Stages III to XVIII and the Sabah sample Stages I to XVII, the differences are not attributable to differences in age.

The ventral fins of Sarawak larvae are colorless, those of North Bornean larvae usually have one or two black spots near the tip.

Range.—Northern and western Borneo.

SABAH: Kota Belud District, Kiau; Kudat District, Bongon; Ranau District, Sungei Kepungit, Sungei Liwagu, Sungei Mamut. SARAWAK: Second Division, Lupar River; Third Division, Baleh River near mouth of Putai River, headwaters of Baleh River; Fourth Division, Long Bareh on Sungei Magoh, Long Sinei, Meligong, headwaters of Sungei Patah; Fifth Division, Lawas. KALIMANTAN: Nanga Raun, Sungei Sibau.

Micrixalus baluensis (Boulenger)

Cornufer baluensis Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 449—Mount Kina Balu, Sabah; 1918, *ibid.*, (9), **1**, p. 373; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 241.

Micrixalus baluensis Inger, 1954, Fieldiana, Zool., **33**, p. 348.

Rana sariba Shelford, 1905, Ann. Mag. Nat. Hist., (7), **15**, p. 209—Mount Saribau, Sarawak.

Material examined.—Borneo 67 (2 BM, type of *baluensis*, type of *sariba*; 65 FMNH).

Taxonomic notes.—The only difference I have found between the types of *Cornufer baluensis* Boulenger and *Rana sariba* Shelfordi is size. The latter specimen is a female 38 mm. snout to vent, which is 9 mm. larger than any other in the extensive sample studied. The synonymy must be treated as tentative.

Reasons for associating this species with the genus *Micrixalus* are given elsewhere (Inger, 1954A).

Description.—A small frog, adult females to 40 mm.; head broader than long; snout rounded; canthus rounded; lores oblique; tympanum distinct, two-fifths to one-half diameter of eye; vomerine teeth in small patches.

Tips of fingers enlarged into truncate disks; disks with circummarginal grooves; disks smaller than tympanum; fingers with narrow fringes of skin; no supernumerary metacarpal tubercles. Disks of toes wider than those of fingers; toes broadly webbed to subarticular

tubercles or slightly beyond on first and second toes; third toe broadly webbed to distal subarticular tubercles, fourth toe to middle subarticular tubercles, fifth toe to distal subarticular tubercle or to base of disk; a ridge of skin on outer edge of fifth toe; an oval inner, but no outer metatarsal tubercle; tibia 0.48–0.56 of snout-vent length.

Skin above coarsely shagreened; a supratympanic fold; throat feebly granular, belly coarsely granular.

Color (in alcohol) reddish brown above, with indistinct darker markings; lips barred; below cream-colored; throat and, less frequently, chest spotted; limbs with dark crossbars.

Secondary sex characters.—Males have small round vocal sac openings in the floor of the mouth, but lack nuptial pads or other specialized asperities. Two males having vocal sacs measured 20.5 and 21.0 mm.

Mature females are larger; those having mature oviducts measured 23.6–29.3 mm., exclusive of the larger type of *R. sariba.* The eggs are very large (2.2–2.5 mm.), non-pigmented, and few in number (eight in the left ovary of one female).

Ecological notes.—The 65 recently collected frogs were caught at three widely separated areas in hilly forest within 500 meters of sea level. The holotype was found between 500 and 900 meters above sea level. Specimens have been caught along small forest streams (47), in hill-top pools (4), and on the forest floor away from water (3). During daytime (8:00 A.M.–4:30 P.M.) frogs were captured only under rocks or floor debris (23) or in water (3). Only at night were frogs caught in exposed situations.

Range.—Borneo.

SABAH: Kota Belud District, Saiap. SARAWAK: Second Division, Saribau; Third Division, Nanga Tekalit; Fourth Division, Nyabau Forest Reserve, Sungei Pesu.

Amolops Cope

The type species, *Polypedates afghanus* Günther (by original designation in Cope, 1865), has a torrent-adapted tadpole bearing an abdominal sucker[1] (Boulenger, 1887C; Annandale and Hora, 1922; Bhaduri, 1935). Boulenger based the identification on similarities between metamorphosing larvae and adults. Thus Noble's (1931) definition of *Staurois* in reality applies to *Amolops.* As Pope and Boring (1940)

[1] In order to avoid repetition of this long phrase, I shall refer to larvae of this sort as gastromyzophorous."

and Liu (1950) based their allocation of species in this group on Noble's interpretation, the Chinese species designated by them as *Staurois* should also be placed in *Amolops*.

Noble's opinion (1927, 1931) that the species having gastromyzophorous tadpoles (figs. 51–54) should be grouped in a separate genus still appears valid. As Noble pointed out, these are the only larvae in the Order Salientia having this particular structure. The possession of the abdominal sucker enables these tadpoles to exploit a source of food closed to other Oriental ranid larvae, namely, the algae growing on the surface of rocks in clear, swift streams. Thus this group of species has undergone a major genetic change that has resulted in a distinct, complex morphological adaptation having significant ecological and behavioral consequences.

Morphologically, adults of *Amolops* as a group are not readily distinguished from those of the *Hylarana* section of *Rana*. Yet the radical differences between the larvae of these two groups of species attest to the genetic differences between the two stocks. The most consistent morphological differences between adults of *Amolops* and *Rana* (*Hylarana*) are in secondary sex characters. Males of *Amolops* never have humeral glands, which are uniformly present in males of *Rana* (*Hylarana*). On the other hand, males of *Amolops* often have gular pouches associated with the vocal sacs, whereas *Rana* (*Hylarana*) males never do.

Griffiths (1963) rejects the separation of these ranids[1] on the basis of their larval modifications because similar larvae appear in the hylid genus *Nyctimystes*. The tadpoles of *Nyctimystes* have expanded lips, but as Griffiths' own illustration shows, they do not have an abdominal ring of cornified epidermis nor the raised rim that delimits the abdominal sucker in *Amolops* larvae. Furthermore, as the collective genotype of the family Hylidae has been separated from that of the family Ranidae for tens of millions of years, larval modification in the Hylidae is not relevant to the problems of classification within the family Ranidae. Griffiths seems to be in error both on theoretical and factual grounds.

Two Bornean species, *Rana cavitympanum* Boulenger and *Hylorana jerboa* Günther, have gastromyzophorous larvae and clearly belong in the genus *Amolops*. Advanced larvae of the first species have distinctive characters of the adults (see below). A metamorphosing frog (FMNH 137865) has all of the characteristics of adult *jerboa*,

[1] Griffiths uses the name *Staurois* in the sense of Noble, which is equivalent to *Amolops* of this paper.

yet still has the abdominal sucker. A third species, *kinabaluensis*, agrees with adults of *jerboa* and *cavitympanum* in secondary sex characters that differentiate adults of the last two from species of the *Hylarana* section of *Rana*; on this basis, *kinabaluensis* is also placed in *Amolops*.

A fourth species having a gastromyzophorous larva, *Amolops larutensis* (Boulenger), has been reported (Boulenger, 1912) from Borneo on the basis of a single specimen (BM 1903.2.21.28) obtained by Marius Jensen, who received the specimen from the collector, Johannes Waterstredt (information from Miss A. G. C. Grandison, British Museum). According to Flora Malesiana (1950, **1**, p. 263), Jensen was in Singapore and Malaya in 1901 but not in Borneo. Although Waterstredt had made zoological collections in Borneo in 1890–1900, in 1901 he collected in Pahang, Malaya for seven months, but not in Borneo (*ibid.*, p. 561). As Jensen got the frog from Waterstredt during the year the latter collected in Malaya, it is much more reasonable to assume that the questionable specimen came from Malaya where the species has been obtained by many collectors in various years than that it came from Borneo where the species has not otherwise been caught.

The adults of Bornean species tentatively assigned to *Amolops* may be distinguished on the following basis:

1A. Tympanum set in a depression on side of head (fig. 50) . . . . *cavitympanum*.
B. Tympanum superficial . . . . 2.

2A. No outer metatarsal tubercle on foot; tibia usually shorter than distance between tympanum and vent . . . . *kinabaluensis*.
B. Outer metatarsal tubercle present; tibia longer than distance between tympanum and vent . . . . *jerboa*.

At least six species of gastromyzophorous ranid larvae have been collected in Borneo. Although several have been assigned to species of adults (Mocquard, 1890; Boulenger, 1893A) on the basis of similarities of advanced tadpoles to adults in limb characteristics, each of these "identified" tadpoles can, with one exception, be assigned with equal justification to two species of adults. In some cases, several distinct forms of tadpoles have, with equal lack of certainty, been assigned to one species of adult.

The single exception is the tadpole assigned to *Amolops cavitympanum* (Boulenger, 1893A). First recorded by Boulenger from Bongon, Sabah, and since collected in northern and central Sarawak (FMNH 83021, 136335; SM unnumbered) and in eastern Kalimantan (RMNH unnumbered), this larval form has a light line on the

tibia such as is found only in *cavitympanum* adults out of all the Bornean species of ranids having enlarged disks at the tips of fingers and toes.

The ambiguity of other larval identifications can be illustrated by analysis of two attempts at specific allocation. The limb characters used by Mocquard (1890) as the basis of his identification of the larvae of *Ixalus nubilus* (=*Staurois natator*) were: toes fully webbed, outer metatarsals separated, one metatarsal tubercle, and first and second fingers of equal length. The single metatarsal tubercle and the relative lengths of the fingers make an assignment to *kinabaluensis* more likely.

Boulenger (1893A) identified as *Rana jerboa* Javan larvae having tooth row counts (as emended by Smith, 1930) of IV:4–4/2–2:V. Van Kampen (1923) assigned Sumatran larvae having tooth row counts of III:4–4/1–1:VII to IV:4–4/1–1:VIII to the same species. A widespread Bornean tadpole having counts of III:3–3/1–1:V could as logically be identified as *jerboa*. The Bornean tadpoles have ribbed, divided beaks, whereas the Sumatran and Javan larvae have smooth, undivided ones. The only justification Boulenger gave for his allocation was the fully webbed toes of his larvae; this is not an adequate diagnosis of *jerboa* now. Van Kampen relied completely on the presence of adult *jerboa* at the collecting site of his tadpoles; this coincidence is not convincing evidence. Furthermore, advanced tadpoles in van Kampen's series (ZMA 5092), which I have examined, differ from adult jerboa in having fringes on the outer fingers and in lacking an outer metatarsal tubercle.

The Bornean larvae (larvae "A": FMNH 77571, 83024, 96012, 136324–31, fig. 53) that probably belong to *jerboa* include all stages from prior to limb bud formation to eruption of fore limbs (Stage XX). The most advanced tadpoles have an outer metatarsal tubercle on the fully webbed feet, the disk of the third finger less than twice as wide as that of the first, the length of the last phalanx greater than the width of its disk, and no fringes on the outer fingers. These four characters in combination fit only *jerboa* among Bornean ranids. But one may question whether the fingers are fully developed; the beaks and teeth, though eroded, are still larval. Unfortunately these larvae cannot be related with complete certainty to the metamorphosing frog mentioned above (p. 257) that is without doubt a young *jerboa*.

Similar doubts surround tentative identifications of other forms of these torrent-adapted tadpoles. Only the rearing of completely metamorphosed young with concomitant preservation of develop-

mental stages or successful artificial fertilization and rearing of embryos to limb bud stages can solve these problems of tadpole identification.

Rather than contribute further to the confusion caused by unwarranted identifications, I am not assigning specific names to these Bornean rhyacophilous larvae (except those of *cavitympanum*). They are described below (p. 270 ff.) and their most likely associations given. They may be distinguished from one another by the following key.

1A. Neither beak divided (fig. 51) .... *Amolops cavitympanum*.
B. One or both beaks divided .... 2.

2A. Both beaks divided (figs. 52 and 53) .... 3.
B. Only upper beak divided (fig. 54) .... 5.

3A. Caudal muscle yellowish green (in life) or white (in preservative) with separated, large, black spots (fig. 52); no spinose tubercles on dorsum ...... *larva* A.
B. Without above pattern; dorsal surfaces various .... 4.

4A. Tooth rows on upper lip III:3–3; dorsum with numerous small spinose tubercles .... larva B.
B. Tooth rows on upper lip I:3–3 or II:3–3; dorsum usually without spinose tubercles .... larva C.

5A. No glands in the ventral fin; each half of upper beak with 12–18 serrae or teeth in tadpoles having developing hind limbs .... larva D.
B. A row of glands in ventral fin near its origin; each half of upper beak with 6–10 serrae in tadpoles having developing hind limbs .... larva E.

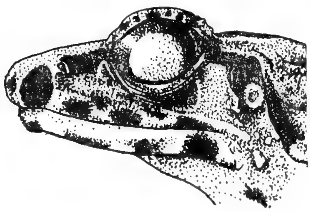


FIG. 50. Side of head of *Amolops cavitympanum*.

Amolops cavitympanum Boulenger

Rana cavitympanum Boulenger, 1893, Proc. Zool. Soc. London, **1893**, p. 525, pl. 43, fig. 1—Kina Balu, Sabah; 1920, Rec. Indian Mus., **20**, p. 193; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 211.

Material.—Borneo 4+11 larvae (2+6 larvae FMNH; 1 larva RMNH; 2+4 larvae SM).

Description.—Body slender; legs long, slender; adult males 42–48 mm.; head longer than broad, obtusely pointed; snout equal to eye diameter, rounded in profile, not projecting; nostril equidistant be-

tween eye and tip of snout or slightly nearer latter; interorbital narrower than eyelid; tympanum visible, set deep in cavity on side of head (fig. 50); vomerine teeth in transverse or slightly oblique groups between choanae, groups equidistant from choanae and each other, separated by slightly less than length of one group.

Tips of fingers dilated into disks, those of outer fingers twice width of other phalanges; third disk equal to diameter of tympanum; disks with circummarginal grooves; first finger longer than second; a weak fringe of skin on inner edges of second and third fingers; a weak supernumerary tubercle on outer metacarpal. Tips of toes dilated into disks slightly narrower than those of outer fingers; broad web reaching disks of all toes; a small, oval inner metatarsal tubercle; a small outer one present or absent; tibia 0.73–0.75 of snout-vent.

Skin above smooth; sides with numerous oval glands, including several in dorsolateral region but no dorsolateral fold; a thick supratympanic fold from eye to axilla; throat and chest smooth; abdomen rugose posteriorly.

Color (in alcohol) dark purplish brown above with or without irregular light spots; light dorsolateral stripe edged below by a dark line; side light gray with small dark spots; side of head gray; a black loreal spot below canthus; lips barred with black; limbs gray above with light-edged blackish crossbars; tibia with cream-colored line on inner margin; below uniformly whitish.

Secondary sex characters.—The single female seen measures 74.6 mm., the four adult males 42.4–47.6 mm. Males have paired subgular vocal sacs having round opening far back in the mouth. The skin at the corners of the throat is thin and wrinkled and forms a bag over the inflated vocal sac. A yellowish nuptial pad covers the dorsal and medial surfaces of the first metacarpal.

Larvae.—Four series of tadpoles (fig. 51) from Sarawak and Kalimantan agree with the one mentioned by Boulenger (1893A). They include stages from pre-limb bud to the beginning of tail resorption. The two in the last stage agree with adults in limb form and proportions and in coloration, including the distinctive light tibia line, while still retaining the larval oral apparatus.

Body oval, flattened, width about three-fifths head and body length; eyes and nostrils dorsal; eye-nostril distance shorter than internarial, which is shorter than interorbital; distance from nostril to tip of snout almost twice internarial.

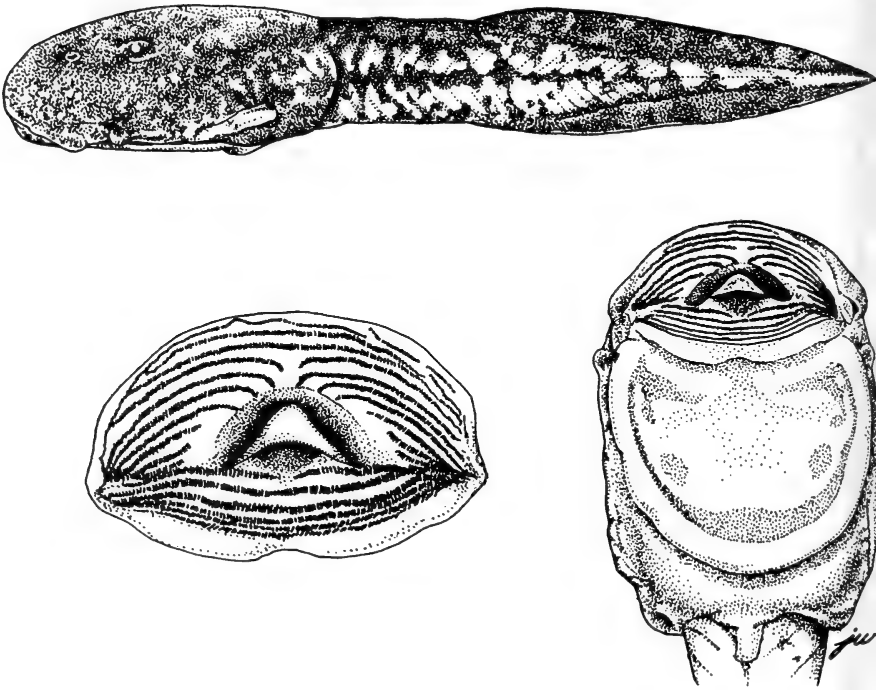


FIG. 51. Tadpole of *Amolops cavitympanum* from Sarawak.

Oral disk ventral, followed by suctorial disk covering almost all of the ventral surface of the body; lips without papillae at all stages; labial teeth II:8–8/2–2:IV (1 specimen), III:8–8/1–1:V (7), III: 8–9/1–1:V (1), III:9–9/1–1:V (2); beaks well-developed, smooth, neither divided, edges finely serrated, anterior black at margin only, posterior black in distal two-thirds.

Suctorial disk with a marginal band of cornified epidermis (Bhaduri, 1935) extending around the entire circumference; usually two patches of similar tissue medial from the marginal band.

Spiracle sinistral, at end of long tube (3.2 mm. in a tadpole 17.0 mm., head-plus-body) at ventrolateral border of body; opening of spiracular tube almost at end of body; anus at end of short tube; a long, narrow poison gland in posterior third of body along ventrolateral edge; skin above smooth, without asperities or spinules.

Tail heavy, tapering gradually to a point; dorsal fin beginning one-third of tail length behind body, equal to or deeper than caudal muscle only in distal fourth; ventral fin beginning behind origin of dorsal, lower than dorsal fin.

Color (in alcohol) of head and body dark slate with obscure lighter marbling; ventrally head and body cream-colored except for beaks, teeth, and brownish cornified areas of suctorial disk; tail purplish with lighter areas forming longitudinal bands on muscle and at bases of fins.

The sizes and body proportions of ten larvae were as follows:

Stage	Head-plus-body	Tail–head-plus-body
pre-limb bud	16.9	1.63
II	18.9	1.55
X	22.0	1.68
XVI	22.7	1.67
XVIII (3)	22.6–24.5	1.43–1.94
XIX	24.0	1.56
XX (2)	22.4–23.1	1.01–1.10

Ecological notes.—The few specimens known are from the forested hilly country of central Borneo. The type is from uncertain elevation on Mount Kina Balu (Boulenger, 1893A); the ones examined were collected between 100 and 900 meters above sea level.

The strikingly modified tadpole is an inhabitant of clear, swift streams having rocky bottoms. Small streams of this sort are common over vast areas of Borneo.

Range.—Known only from Borneo.

SABAH: Kota Belud District, Mount Kina Balu (*ibid.*); Kudat District, Bongon (*ibid.*); Ranau District, Sungei Mamut. SARAWAK: Third Division, Sungei Sujai, headwaters of Baleh River, Mengiong River; Fourth Division, Kelabit Plateau, Meligong, Long Sinei in Akah River valley. KALIMANTAN: headwaters of Mahakam River.

Amolops jerboa (Günther)

Hylorana jerboa Günther, 1872, Proc. Zool. Soc. London, **1872,** p. 599, pl. 40, fig. B—Matang, Sarawak.

Rana jerboa Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 67; 1920, Rec. Indian Mus., **20,** p. 196; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 208; Smith, 1925, Jour. Sarawak Mus., **3,** p. 33; 1931, Bull. Raffles Mus., no. 5, p. 17.

Rana whiteheadi Boulenger, 1887, Ann. Mag. Nat. Nist., (5), **20,** p. 96—Kina Balu, Sabah; Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2,** p. 144 (part); Brongersma, 1937, Zool. Meded., **20,** p. 17.

Material examined.—Borneo 182 (27 BM, including types of *jerboa;* 107 FMNH; 12 MCZ; 11 NSH; 1 RMNH; 14 SM; 2 SNG; 1 SNM; 7 UMMZ); Java 10 (7 SNG; 3 ZMA); Sumatra 7 (4 MZB; 3 ZMA).

Taxonomic notes.—*Rana whiteheadi* was described from four adult males having vocal pouches and a maximum length of 46 mm. (Boulenger, 1887B). Although Boulenger said that his types differed from *jerboa* Gunther, his description fits topotypes of *jerboa* and specimens of the latter from Kina Balu, the type locality of *whiteheadi*. One of the most distinctive characters of *jerboa* is its remarkably long leg. The femoro-tibial joint reaches beyond the shoulder and the tibia is equal to the distance from the eye or anterior rim of the tympanum to the vent. These are the leg measurements attributed by Boulenger to *whiteheadi*. As no other character mentioned in Boulenger's description will distinguish *whiteheadi* from *jerboa*, the former must be reduced to the synonymy of *jerboa*.

Whitehead's entire collection, from which Boulenger's types came, was deposited in the museum in Paris. I have seen three males (MHNP 89.239–241) from that collection. These specimens, which formed part of the series called *whiteheadi* by Mocquard (1890), are 58–65 mm. long and have shorter legs than *jerboa* and the types of *whiteheadi*. The femoro-tibial joint reaches only as far as the shoulder, thus agreeing with Mocquard's figure (plate 10, fig. 2), and the tibia is shorter than the distance between the tympanum and the vent. This series, therefore, differs from the original description of *whiteheadi* and represents a distinct, unnamed species.

The name *whiteheadi* has been applied by van Kampen (1923) and Smith (1931A) to the species figured by Mocquard. I have seen 23 individuals of this shorter-legged form; 17 adult males (with vocal pouches) measure 58–68 mm. and six females 75–93 mm. Only one of the 40 adult *jerboa* males I have measured exceeds 46 mm.; 31 *jerboa* females have a size range of 60–82 mm., though only two exceed 75.0 mm. The maximum of Boulenger's *whiteheadi* types, 46 mm., falls in the range of *jerboa* and far outside the range of the shorter-legged frog, which is described below as *Rana kinabaluensis*.

The specimens from northern Burma identified as *Rana jerboa* by Smith (1940) are probably *R. livida* (Blyth). They differ from *A. jerboa* in having single, long, thick rictal glands (a number of small ones in *jerboa*), fingers with a fringe of skin, ova without pigment, and the interorbital wider than the upper eyelid.

I also doubt Boulenger's identification (1893B) of specimens from Karen Bia-Po, Burma, though I have not examined those frogs. Boulenger found no outer metatarsal tubercles, which are invariably conspicuous in typical *jerboa*. The adult male examined by Boulenger had, according to him, a tympanum as wide as the eye and, hence,

wider than the tympanum of male *jerboa* from Borneo. Boulenger did not mention gular pouches, which are so obvious in male *jerboa*, though he did describe the color of the throat (p. 336).

Description.—Body slender, legs extremely long; adult males 31–53 mm., females 60–82 mm.; head triangular, depressed, obtusely pointed, width 0.29–0.34, length 0.36–0.41 of snout-vent; snout equal to eye diameter, projecting in profile; nostril closer to tip of snout than to eye; interorbital narrower than upper eyelid; tympanum conspicuous, ½ to $^3/_5$ eye diameter; vomerine teeth in oblique groups between posterior halves of choanae, groups separated from each other by distance subequal to length of one group, usually farther from choanae.

Tips of fingers dilated into disks less than twice width of phalanges, disk of third finger about half width of tympanum in females; disks with circummarginal grooves; first finger usually longer than second; fingers without fringes or flaps on sides; a weak supernumerary tubercle on each of three outer metacarpals. Tips of toes dilated into disks subequal to those of lateral fingers; broad web reaching disks of all toes; an oval inner and a smaller, round outer metatarsal tubercle; tibia 0.66–0.76 of snout-vent.

Skin coarsely shagreened above; dorso-lateral fold usually visible; a weak fold from above tympanum to axilla; venter smooth or weakly rugose posteriorly.

Color (in alcohol) reddish brown above; blackish just below dorso-lateral fold, becoming lighter lower on side; ventrally cream-colored or whitish, usually immaculate, some individuals with brown spots on throat; legs usually with dark crossbars dorsally.

Sides, posterior half of abdomen, and underside of legs yellowish green in life.

Secondary sex characters.—Females are much larger than males. In the Bornean sample, the smallest female containing mature, pigmented ova measures 59.8 and the largest 82.3 mm.; the mean of 18 females is 67.09±1.31 mm. Males with vocal sacs vary from 30.9 to 53.0 mm.; the mean of 40 is 36.40±0.38 mm. The sexes do not differ in head size or shape or in the length of leg. They do differ in the relative size of the tympanum; the ratio of tympanum to snout-vent in males varies from 0.088 to 0.107 (medium 0.100; N=17), in females from 0.056 to 0.071 (median 0.062; N=11).

Males have paired subgular vocal sacs, each sac restricted to the extreme lateral corner of the throat. The skin in this area is thrown into conspicuous folds, but it is not connected with the muscle sur-

rounding the vocal sac or with the sac itself. The nuptial pad is a yellowish structure covering the dorsal and median surfaces of the first finger from its base to the level of the subarticular tubercle. Males lack humeral glands, lineae masculinae, and distinctive asperities.

Ecological notes.—This long-legged nocturnal frog lives along swift hill or mountain streams in forested country. It usually sits on moist rocks or vegetation right at stream edge. When disturbed it jumps from boulder to boulder, each leap being two or more meters long.

The altitudinal distribution of *jerboa* is extensive. Smith (1931A) records it from Mount Kina Balu at elevations between 900 and 2200 meters, with about four-fifths of his specimens coming from 1000 meters or below. The Bornean material seen, excluding Kina Balu specimens, are from elevations between 100 and 600 meters above sea level. Mertens (1934) refers to *jerboa* as a typical montane frog. Its abundance on Borneo below 1000 meters suggests that its distribution is related to the presence of swift, rocky streams rather than high elevations. Such streams occur in Borneo in many places of moderate or low elevations.

Judging by the secondary sex characters, the breeding season in Borneo is extensive. Available males were collected from April through August and all had well-developed nuptial pads. All but one of the females collected June through August contained enlarged ova; one had eggs in the oviduct.

Geographic variation.—Specimens from Java and Sumatra resemble those from Borneo in all characters studied.

Range.—Malay Peninsula (Boulenger, 1912), Sumatra, Borneo, and Java.

SABAH: Kota Belud District, Kamborangah (Smith, 1931A), Kenokok, Kiau (*ibid.*), Lumu Lumu, all on Mount Kina Balu; Lahad Datu District, Sungei Pangaruan; Ranau District, Sungei Liwagu, Sungei Mamut, Tenompok. SARAWAK: First Division, Mount Gadin (Smith, 1925B), Matang, Tandjong Datu; Second Division, Lupar River valley; Third Division, upper Baleh River, Mengiong River; Fourth Division, Meligong, Patah River, Long Sinei; Fifth Division, Lawas. KALIMANTAN: Long Petah.

Amolops kinabaluensis new species

Rana whiteheadi (non Boulenger) Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 144 (part), pl. 10, fig. 2; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 210; Smith, 1931, Bull. Raffles Mus., no. 5, p. 17.

Holotype—Field Museum of Natural History number 109798, an adult male from Kiau, Mount Kina Balu, Sabah. Collected by F. N. Chasen and H. M. Pendlebury, April, 1929.

Diagnosis.—A large *Amolops* (to about 95 mm., snout-vent); head large, body stocky, especially in females; digits with well-developed disks; fingers without lateral fringes of skin; toes webbed to disks; no outer metatarsal tubercle; tibia usually shorter than distance between tympanum and vent; males with gular pouches at corners of throat.

Description of holotype.—Head broad, body and legs slender; snout obtusely pointed, projecting slightly; canthus distinct; lores nearly vertical, concave; nostril nearer to tip of snout than to eye; eye large, equal to snout; interorbital narrower than upper eyelid; tympanum conspicuous, about two-fifths eye diameter; vomerine teeth in strong oblique groups beginning between choanae and extending beyond their posterior level, groups separated from each other by less than length of one group, farther from choanae.

Fingers with broad disks about twice width of phalanges, disk of third finger about two-thirds diameter of tympanum; disks with circummarginal grooves; first finger longer than second; fingers without fringes of skin; a weak supernumerary tubercle on outer metacarpal. Tips of toes dilated into disks like those of fingers but smaller than that of third finger; broad web reaching disks of all toes; outer metatarsals separated by web to their bases; oval inner metatarsal tubercle about one-third length of first toe; no outer metatarsal tubercle.

Skin smooth above, with narrow, interrupted dorsolateral fold; a weak supratympanic fold from eye to axilla; ventral surfaces smooth except for rugose skin posteriorly on abdomen.

Color (in alcohol) dark brown above, with indistinct small, darker spots on back, on dorsolateral fold, and on supratympanic fold; limbs with dark crossbars; below yellowish-white suffused with brown, especially on throat; legs pale brown below.

Measurements (mm.): snout-vent 64.5; tibia 42.4; head length 24.6; head width 22.7; tympanum 4.1.

Paratypes.—BM 95.11.7.79, FMNH 109799-800, MHNP 89.239-41, NMB 4705-09, SNM 264, 274, 279, 327, 338, 351, 368, 402, plus two unnumbered. All from Mount Kina Balu.

These frogs range in size from 58.1 to 92.8 mm. They agree with the holotype in almost all details. Variation is limited to body proportions and those characters showing sex dimorphism. The ratio of

head width to snout-vent varies from 0.316 to 0.376 (median 0.351); the ratio of tibia to snout-vent is 0.607–0.675 (median 0.647).

Smith (1931A) describes the color in life as follows: "Above dark green except hind limbs which are brownish. Head and trunk spotted with bright yellow. Underside of trunk silvery white; limbs brownish."

TABLE 33.—Sex dimorphism in body proportions of *Amolops kinabaluensis* applying Mann-Whitney U test. Proportions given in thousandths of snout-vent length.

Sex	No.	Range	Median	U	P
		Tympanum/snout-vent			
Males	15	58–65	61	0	<0.001
Females	4	49–51	50		
		Head length/snout-vent			
Males	14	372–399	384	2	0.002
Females	5	352–378	371		
		Head width/snout-vent			
Males	15	316–368	351	25	>0.10
Females	5	329–376	345		

Secondary sex characters.—Females are about 25 mm. longer than males. Five females, all containing enlarged, pigmented ova, measure 74.7–92.8 mm. (mean 88.08 ± 3.45 mm.); 17 males having vocal sacs measure 58.1–68.2 mm. (mean 63.57 ± 0.52 mm.). The tympanum and head length are relatively larger in males (Table 33).

All the males examined have paired subgular vocal sacs having round openings into the mouth just inside the commissure of the jaws. Each vocal sac and its investing muscle bulges out at the angle of the jaw into a large, wrinkled pouch of gular skin.

The nuptial pad is a pale yellowish gray velvety structure covering the dorsal and median surfaces of the first finger from its base to the level of the subarticular tubercle. The pad continues beyond that point as a narrow strip along the median edge of the finger to the base of the terminal phalanx or just beyond.

No additional asperities, glands, or lineae masculinae were seen.

Ecological notes.—The long legs, completely webbed toes, and large digital disks suggest that *kinabaluensis*, like *jerboa*, lives on rocks along swift streams. All specimens for which data are available were caught between 900 and 1000 meters above sea level.

The ova are large (2.0–2.5 mm.) and have a pigmented hemisphere.

Comparisons.—The combination of dorsolateral folds, large grooved disks on the fingers, and completely webbed toes distinguishes *kinabaluensis* from all Bornean ranids except *Rana hosei, R. chalconota, Amolops cavitympanum* and *A. jerboa.*

The resemblance is closest with *Rana hosei* in habitus and size. Both have moderately stocky bodies and large heads and are dark green in life. Adult males of *hosei* are 47–60 mm., as compared to 58–68 in *A. kinabaluensis;* females are 82–95 and 75–93 mm., respectively. *Rana hosei,* however, differs from *A. kinabaluensis* in having distinct flaps of skin along the inner edges of the second and third fingers, a distinct supernumerary tubercle on each of the three outer metacarpals, and a light stripe on the upper lip. Though males of *hosei* have vocal sacs, they lack the distinct gular pouches found in *kinabaluensis.*

Rana chalconota is smaller than *A. kinabaluensis,* males and females of the former being 33–44 and 46–60 mm., respectively, or 20 to 30 mm. smaller than the corresponding sizes of *kinabaluensis. Rana chalconota* further differs from *A. kinabaluensis* in having flaps of skin on the edges of the second and third fingers, distinct supernumerary tubercles on the three outer metacarpals, a distinct outer metatarsal tubercle, and humeral glands in the males.

As already noted (p. 264), *A. jerboa* is smaller and has longer legs than *kinabaluensis.* These two species also differ in head width and diameter of tympanum (Table 34). A distinct outer metatarsal tubercle is present in *jerboa* but not in *kinabaluensis.*

Amolops cavitympanum differs from *kinabaluensis* in having a deeply sunken tympanum, flaps of skin on the inner edges of the second and third fingers, and a barred lower lip.

TABLE 34.—Comparison of body proportions of *Amolops jerboa* and *A. kinabaluensis.* Proportions given in thousandths of snout-vent.

	Males			Females		
	No.	Range	Median	No.	Range	Median
			Tympanum/snout-vent			
jerboa	17	88–107	100	11	56–71	62
kinabaluensis	15	58–65	61	4	49–51	50
			Tibia/snout-vent			
jerboa	16	669–751	723	13	660–758	726
kinabaluensis	15	607–675	655	4	622–653	626
			Head width/snout-vent			
jerboa	10	289–329	319	10	309–336	322
kinabaluensis	15	316–368	351	5	329–376	345

Range.—Known only from the type locality in Sabah.

Amolops larva A. Figure 52.

Material examined.—Borneo 14 lots (1 BM; 13 FMNH).

These series include all phases of development from prior to visible limb bud to metamorphic stages. The most advanced larvae have largely resorbed their tails while the ventral suctorial disk and larval oral apparatus are still present.

Description.—Body oval, depressed, broadly rounded anteriorly, length 1½ times width; eyes and nostrils dorsal; diameter of eye equal to eye-nostril distance; interorbital 1½ times diameter of eye; nostril almost twice as far from tip of snout as from eye; spiracle sinistral, ventrolateral, at end of free tube; end of spiracular tube about 1½ times as far from eye as from end of body.

Oral disk ventral, followed by large suctorial abdominal disk; distance between abdominal disk and end of body 0.15–0.25 of head-

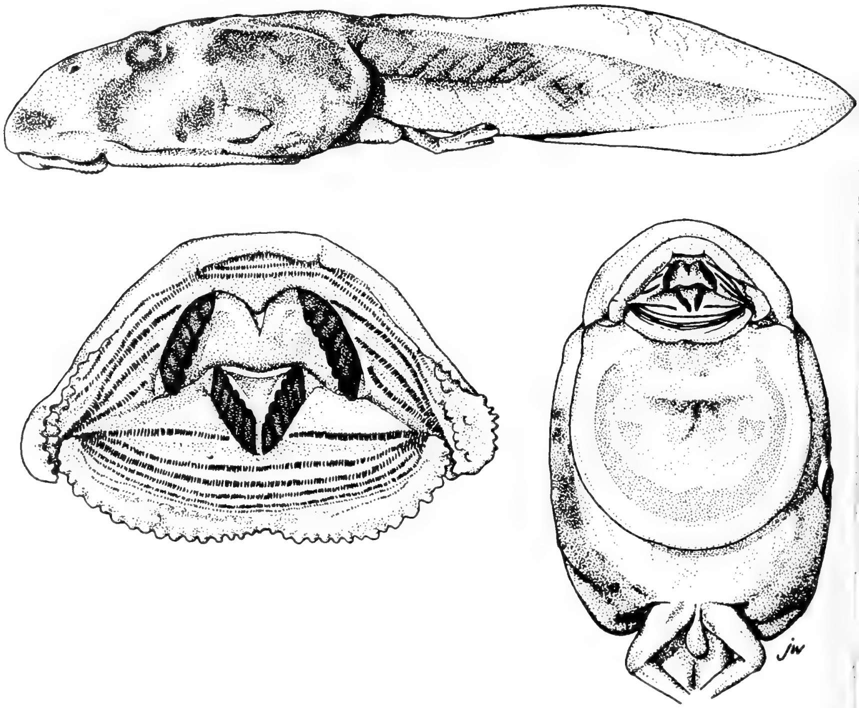


FIG. 52. Tadpole of *Amolops* sp. A from Sarawak.

plus-body length; short papillae in a single row at lateral margin of upper lip and across entire margin of lower lip; a second row of short papillae medially at corners of oral disk; upper labial teeth II:3–3 (13 specimens) or III:3–3 (5) in the larvae younger than Stage III, III:3–3 (19), III:3–4 (2), or III:4–4 (1) in larvae older than Stage IV; tooth rows on lower lip 1–1:III (1), 1–1:IV (6), or 1–1:V (7) in pre-limb bud larvae, 1–1:V in larvae having developing hind limbs; both beaks completely black, divided, and strongly ribbed; base of upper beak M-shaped; each half of upper beak with six to 10 serrae.

Tail convex dorsally, tapering gradually, 0.56–0.63 of total length; caudal muscle thick; dorsal fin beginning at a distance behind end of body, rising steeply, deeper than caudal muscle in distal half of tail; ventral fin not as deep as dorsal, beginning behind origin of dorsal.

Skin smooth; a patch of large glands ventrolaterally behind head, a smaller patch behind eye, a larger patch on side at end of body; no glands in either fin.

Color (in life) greenish yellow on body and tail, with large black spots on body and caudal muscle; both fins with a fine dark network.

Size at various stages of development are given in Table 35.

TABLE 35.—Sizes at various developmental stages of larvae of *Amolops* larva A.

Stage	No.	Head-plus-body	Total
pre-limb bud	14	3.2–7.3	—
II	4	7.5–9.3	19.6–22.6
V	1	8.3	20.5
VIII	1	12.1	29.7
X	2	11.9–12.2	28.3 (1)
XI–XIII	12	13.0–14.5	32.0–34.1
XIV–XVI	4	14.2–15.4	33.0–37.0
XVII	2	14.3–14.6	33.2–34.2
XX	3	14.9–15.7	21.6–29.6

Relations.—The most advanced larvae have the tips of the digits expanded into disks, all toes fully webbed to the disks, a distinct outer metatarsal tubercle, and no fringes along the edges of the fingers. Only two Bornean ranids have all of these characteristics: *Amolops jerboa* and *A. cavitympanum*. Larvae of *cavitympanum*, described on p. 261, differ from those under discussion here in coloration, skin texture, form of beaks, and tooth counts.

Two other gastromyzophorous larvae also resemble adult *A. jerboa* in limb characteristics (see larvae "B" and "C" below).

Ecological notes.—These larvae live in swift, clear water of small to moderate-sized (ca. 2–20 meters wide) forest streams, but only

where the stream bed consists of large stones or bed rock. By day the larvae are seen singly or in twos or threes. By night, however, they form aggregations of 25 to more than 100. The aggregations form on the upper surface of large rocks, usually a single cluster to a rock and often with only a thin film of water flowing over the tadpoles. The orientation of larvae in aggregations varies though in all cases they were in a single layer. In two aggregations the tadpoles were arranged with their heads pointing outward from the center; in a third they were all facing upstream. Orientation in other clusters was not recorded.

Localities.—SARAWAK: First Division, Matang (FMNH 77571, 77573); Third Division, headwaters of Baleh River (FMNH 96012), Mengiong River (FMNH 136324–31, 136333); Fourth Division, Long Sinei (FMNH 83024); no specific locality (BM 1933.6.20.1–3).

Amolops larva B. Figure 53.

Material examined.—Borneo 5 lots (FMNH).

These specimens span developmental stages from the beginning of visible limb bud to eruption of fore limbs.

Description.—Body oval, depressed, broadly rounded anteriorly, length about 1½ times width; eyes and nostrils dorsal; diameter of eye slightly greater than eye-nostril distance; interorbital 1½ times diameter of eye; nostril about twice as far from tip of snout as from eye; spiracle sinistral, ventrolateral, at end of free tube; end of spiracular tube as far from eye as from end of body.

Oral disk ventral, followed by large suctorial disk; distance between disk and end of body 0.15–0.24 of head-plus-body length; short papillae in a single, continuous row at margin of lower lip; a similar row on margin at lateral third of upper lip; a second row of short papillae medially at corners of oral disk; upper labial teeth (in larvae with developing limbs) III:3–3 (22 specimens), III:3–4 (1), and II:3–3 (1, Stage I); lower labial teeth 1–1:IV (7), 1–1:V (11), 1–1:VI (6); both beaks completely black, divided, strongly ribbed; base of upper beak M-shaped; each half of upper beak with 5–9 serrae.

Tail convex dorsally, tapering gradually, 0.57–0.64 of total length; caudal muscle thick; dorsal fin beginning a short distance behind end of body, rising gradually or steeply, deeper than muscle in distal two-fifths or third of tail; ventral fin not as deep as dorsal, beginning after proximal third of tail.

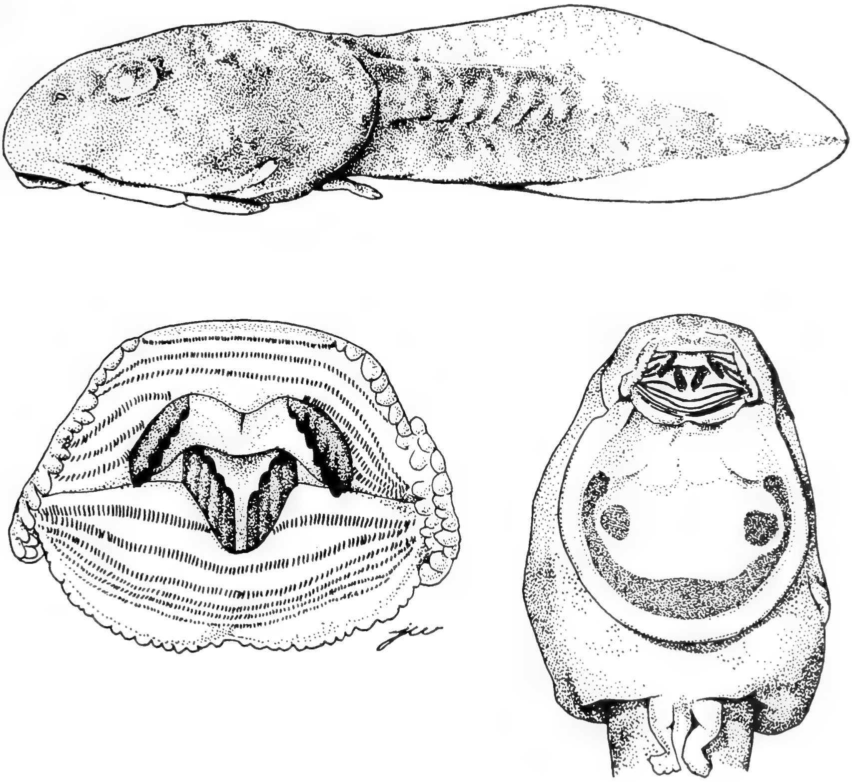


FIG. 53. Tadpole of *Amolops* sp. B from Sabah.

Skin with numerous small, spinose tubercles dorsally and laterally on head and body in stages beyond foot paddle; a small patch of glands ventrolaterally below eye, similar patches ventrolaterally at rear of head, laterally behind eye, and laterally at end of body; a row of two to five glands at base of ventral fin just beyond its origin.

Color (in alcohol) of head and body of tadpoles in earliest stages of limb development pale cream-colored with broad median, black streak running from tip of snout to occipital region, a black streak from below eye to snout, and a small black dorsolateral spot at rear of head; dark areas expanding to cover all of dorsal and lateral surfaces of head and body as tadpoles develop; caudal muscle in all tadpoles dark gray with irregular black mottling except for immaculate cream-colored ventral surface proximal to origin of ventral fin, ventral margin of dark area irregular; both fins with faint mottling.

Sizes at various stages of development are:

Stage	No.	Head-plus-body	Total
I	2	8.5– 9.7	20.9–23.6
III–V	3	9.5–11.2	22.3–26.7
IX–XI	7	12.1–13.7	29.7–33.7
XIV–XVI	5	12.4–15.7	33.7–43.7
XVII–XVIII	6	15.2–17.0	37.4–46.8
XX	1	16.3	39.1

Relations.—Advanced larvae (stages XVIII–XX) have outer metatarsal tubercles, toes completely webbed to the disks, first finger slightly shorter than second, disk of the third finger less than twice that of the first finger, and no fringes on the fingers. The fingers and disks are like those of *Amolops jerboa* and *A. kinabaluensis*, but the outer metatarsal tubercle distinguishes them from adult *kinabaluensis*. These tadpoles, therefore, are most similar to adults of *A. jerboa*.

In all of these characters "larva A" is also most similar to *A. jerboa*. But these two larval forms differ from one another in color pattern (especially of the caudal muscle), in spinosity of dorsal and lateral surfaces of head and body, and in the presence or absence of glands in the ventral fin. These two larval forms are not geographic replacements. Specimens (FMNH 136323–26) of both were caught within a radius of three meters in a rocky stream bed.

Localities.—SABAH: Ranau District, Sungei Liwagu (FMNH 131243); Tambunan District, Sungei Kaingeran (FMNH 109493); Tuaran District, 3½ miles E. of Tuaran (FMNH 140283). SARAWAK: Third Division, Mengiong River (FMNH 136322–3).

Amolops larva C

Material examined.—Borneo 1 lot (BM).

Description.—Body oval, depressed, broadly rounded anteriorly; eyes and nostrils dorsal; diameter of eye equal to eye-nostril distance; interorbital greater than diameter of eye; nostril twice as far from tip of snout as from eye; spiracle sinistral, ventrolateral.

Oral disk ventral, followed by large suctorial abdominal disk, distance between abdominal disk and end of body about equal to diameter of eye; short papillae in single row on lateral third of upper lip and across entire margin of lower lip; upper labial teeth I:3–3 (5 specimens) or II:3–3 (1); lower labial teeth 1–1:IV (6); both beaks black, divided, and ribbed.

Tail strongly muscular; fins low, beginning behind body; tail length 0.56–0.58 of total.

Skin above smooth (6 specimens, Stages IV–XX), or with numerous, small, spinose tubercles (1 specimen, Stage XV); a patch of glands ventrolaterally below eye, similar patches ventrolaterally at rear of head, laterally behind eye and laterally at end of body.

Color (in alcohol) of head and body dorsally and laterally grayish brown, without spots; caudal muscle marked with dark brown and yellow, the dark areas predominating; fins mostly colorless, a few small dark areas on dorsal fin.

Head-plus-body 8.2 (Stage IV) to 12.7 mm. (Stage XV); total length 21.0 (Stage VI) to 23.6 mm. (Stage X).

Relations.—These larvae were studied prior to the collection of most of the other forms. As a consequence, the importance of many characters was not appreciated, and my notes are incomplete.

Boulenger (1893A, p. 526, pl. 43, fig. 4) assigned these tadpoles to *Rana whiteheadi* (=*A. jerboa*). As already noted, the two preceding forms, from which larval "species" C differs in labial tooth row counts, can be identified as *jerboa* with equal justification.

Locality.—SARAWAK: First Division, Sarawak River (BM 93.3.6.81–90).

Amolops larva D. Figure 54.

Material examined.—Borneo 4 lots (FMNH). These samples include larvae between Stages II and XIX.

Description.—Body oval, wider at rear, broadly rounded anteriorly, flat below; a large ventral suctorial disk; eyes dorsolateral, not visible from below; diameter of eye equal to or a little greater than eye-nostril distance; interorbital twice diameter of eye; nostril-snout distance 1½ times eye-nostril distance; spiracle sinistral, ventrolateral, at end of free tube, opening of tube slightly closer to end of body than to perpendicular from rear of eye.

Oral disk ventral, followed by abdominal disk; distance between abdominal disk and end of body 0.17–0.23 of head-plus-body length; short papillae in a single continuous row at edge of lips except for middle two-thirds of upper lip; a short row of papillae medially at corners of oral disk; upper labial teeth III:3–3 (2 specimens), III:3–4 (1), or III:4–4 (3); lower labial teeth 1–1:V (1) or 1–1:VI (5); both beaks strongly ribbed and black; upper beak divided, lower beak single; base of upper beak M-shaped; each half of upper beak with 12–18 serrae (Stage VI and beyond), eight in one Stage II larvae.

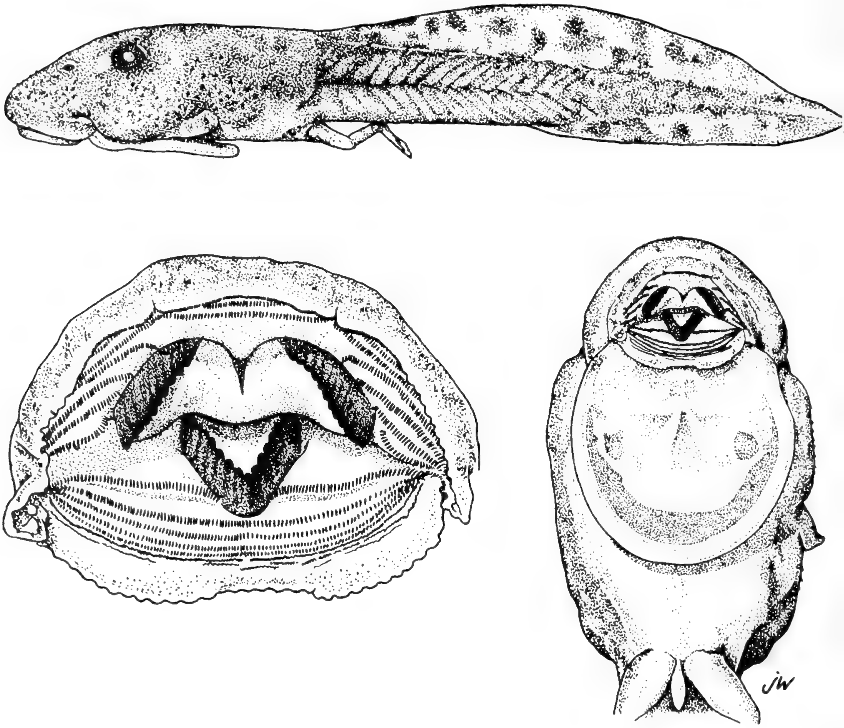


FIG. 54. Tadpole of *Amolops* sp. D from Sarawak.

Tail strongly convex dorsally, tapering gradually to rounded tip, 0.60–0.66 of total length; caudal muscle thick; dorsal fin beginning behind end of body, rising steeply, deeper than caudal muscle only in distal third of tail; ventral fin not as deep as dorsal, origin behind that of dorsal.

Skin of snout in Stage II tadpole with a few conical spines; entire dorsal surface of head and body in larvae in Stage VI and beyond densely strewn irregularly with conical spines; spines without melanin; two small patches of glands ventrolaterally, one at rear of head and one just behind level of mouth; a small patch of glands dorsolaterally at rear of head and one on side at end of body; glands obscured by spinose skin in older larvae; no glands in ventral fin.

Color (in alcohol) of head, body, and caudal muscle brown with dark brown spots; both fins heavily spotted with dark brown.

Total length of Stage II larva 34.6, of Stage XIX larva 73.1 mm.; head-plus-body 13.4 and 24.8, respectively.

The most advanced tadpole has the tips of fingers and toes expanded, no outer metatarsal tubercle, fully webbed toes, and the outer edge of the fifth toe with a fringe of skin. The prepollex is conspicuous as is an outer palmar callosity. The fourth finger has a supernumerary tubercle on the metacarpal. The width of the disk of the third finger is less than the length of the last phalanx (13:16 micrometer units).

Relations.—The Bornean swift-water ranids having fully webbed toes include *Staurois tuberilinguis, Amolops jerboa, A. kinabaluensis A. cavitympanum, Rana hosei, Staurois natator,* and *S. latopalmatus.* Larvae of the last four are known and differ from these in many characters (cf., pp. 190, 247, 253, and 260).

Adults of *Amolops jerboa* have outer metatarsal tubercles, which are lacking in the advanced tadpole of this series. Adult *Staurois tuberilinguis* differ from the advanced tadpole of this series in lacking a prominent prepollex, a supernumerary tubercle on the fourth metacarpal, and a fringe of skin along the outer edge of the fifth toe.

Adults of *A. kinabaluensis,* however, have all of these structures. The ratio of width of the disk to length of terminal phalanx of the third finger in adult *A. kinabaluensis* (0.76–1.00 in three) is close to that of the larva (0.81).

Again the question arises whether the fingers are fully developed in the advanced tadpole. If they are, then this form of tadpole almost certainly should be assigned to *A. kinabaluensis.*

Localities.—SABAH: Ranau District, Sungei Kepungit (FMNH 130892–93); Tambunan District, Sungei Kaingeran (FMNH 109492). SARAWAK: Fourth Division, Long Sinei (FMNH 83023).

Amolops larva E

Material examined.—Borneo 6 lots (FMNH).

These span developmental phases from prior to visible limb bud to Stage XVIII (anal tube resorbed).

Description.—Body oval, depressed, broadly rounded anteriorly, length 1½ times width; eyes and nostrils dorsal; diameter of eye equal to eye-nostril distance; nostril farther from tip of snout than from eye; spiracle sinistral, ventrolateral, at end of free tube; end of spiracular tube slightly farther from eye than from end of body.

Oral disk ventral, followed by large suctorial abdominal disk; distance between abdominal disk and end of body 0.13–0.17 of head-plus-body length; short papillae in a single row at lateral thirds of

upper lip and across entire margin of lower lip; a second row of short papillae medially at corners of oral disk; labial teeth III:4–4/1–1:V (14 specimens) in larvae from Stage V onward; both beaks completely black and ribbed; only upper beak divided; base of upper beak M-shaped; each half of upper beak with four to five serrae in pre-limb bud larvae (2), six to seven in Stages IV–VII (4), seven to ten in Stage VIII to XVIII (11).

Tail convex dorsally, tapering gradually to a rounded end, 0.59–0.64 of total length; caudal muscle thick; dorsal fin beginning at a distance from end of body, rising steeply, deeper than caudal muscle in distal two-fifths or third of tail; ventral fin not as deep as dorsal, beginning behind origin of dorsal.

Numerous small, spinose tubercles dorsally and laterally on head and body in all stages beyond III; a small group of glands ventrolaterally below eye, similar groups ventrolaterally at rear of head, laterally behind eye, and laterally at end of body; a row of three to five glands at base of ventral fin just beyond its origin.

Color (in alcohol) of dorsal and lateral surfaces of head, body, and caudal muscle brown with numerous contiguous black spots; general appearance is blackish brown with a few light areas; both fins with network of melanophores; ventral surfaces of head, body, and caudal muscle immaculate cream-colored.

Sizes (mm.) at various stages of development are:

Stage	No.	Head-plus-body	Total
pre-limb bud	2	5.4	13.2–13.6
V	2	10.2–10.3	27.4–27.6
VII	1	12.2	28.9
IX–XI	3	13.6–14.6	34.8–39.9
XII	2	13.4–14.8	....
XIV	2	14.6–15.7	38.2 (1)
XV	2	15.5 (2)	41.0 (1)
XVIII	1	16.2	41.0

Relations.—The most advanced of these tadpoles (Stage XVIII) has an outer metatarsal tubercle and fully webbed toes. It thus resembles adults of *Amolops jerboa* as do larval forms "A" and "B." The present larvae were collected in the same river system (Sungei Liwagu and tributaries) but not at the same localities as larva "B"; the two forms differ in labial tooth counts and in the form of the lower beak.

Locality.—SABAH: Ranau District, Sungei Mamut (FMNH 130894–99).

RHACOPHORIDAE

Bornean species of the genera *Rhacophorus* and *Philautus* can be distinguished on the basis of vomerine teeth, which are absent in *Philautus* and present in *Rhacophorus*.

Rhacophorus

KEY TO BORNEAN SPECIES (Fig. 55).

1A. Broad webbing reaching disk of fourth finger as a broad sheet (fig. 55A, B) 2.
B. Broad webbing not reaching disk of fourth finger (fig. 55I) . . . . 8.

2A. Broad webbing reaching disk of first finger (fig. 55B) . . . . *nigropalmatus*.
B. Broad webbing not reaching disk of first finger (fig. 55A) . . . . 3.

3A. A distinct ridge or flap of skin along outer edge of forearm (fig. 55C) . . . . 4.
B. No ridge or flap of skin along outer edge of forearm . . . . 6.

4A. A long, pointed dermal appendage at heel (fig. 55D) . . . . *baluensis*.
B. A round, narrow or broad flap at heel (fig. 55E) . . . . 5.

5A. A transverse, dermal projection above vent (fig. 55F) . . . . *dulitensis*.
B. No such appendage . . . . *pardalis*.

6A. Broad webbing reaching almost to disk of second finger on inner side (fig. 55G) *harrissoni*.
B. Broad webbing not reaching beyond subarticular tubercle of second finger on inner side (fig. 55H) . . . . 7.

7A. Tympanum at least $1\frac{1}{2}$ times width of disk of third finger . . . . *rufipes*.
B. Tympanum at most $1\frac{1}{3}$ times width of finger disk . . . . *fasciatus*.

8A. Broad webbing reaching distal subarticular tubercle of fourth finger or slightly beyond (fig. 55I) . . . . 9.
B. Broad webbing not reaching distal subarticular tubercle of fourth finger; often no webbing at all . . . . 11.

9A. No flap or fringe of skin along forearm . . . . *acutirostris*.
B. A distinct flap or fringe on forearm . . . . 10.

10A. A smooth-edged ridge or fringe of skin on forearm (55J) . . . . *dulitensis*.
B. A crenulate fringe of skin on forearm (fig. 55K) . . . . *appendiculatus*.

11A. A bony ridge projecting above tympanum (fig. 55L) . . . . *otilophus*.
B. No such ridge . . . . 12.

12A. A row of conical tubercles on tarsus (fig. 55M) . . . . *everetti macroscelis*.
B. No such tubercles on tarsus . . . . 13.

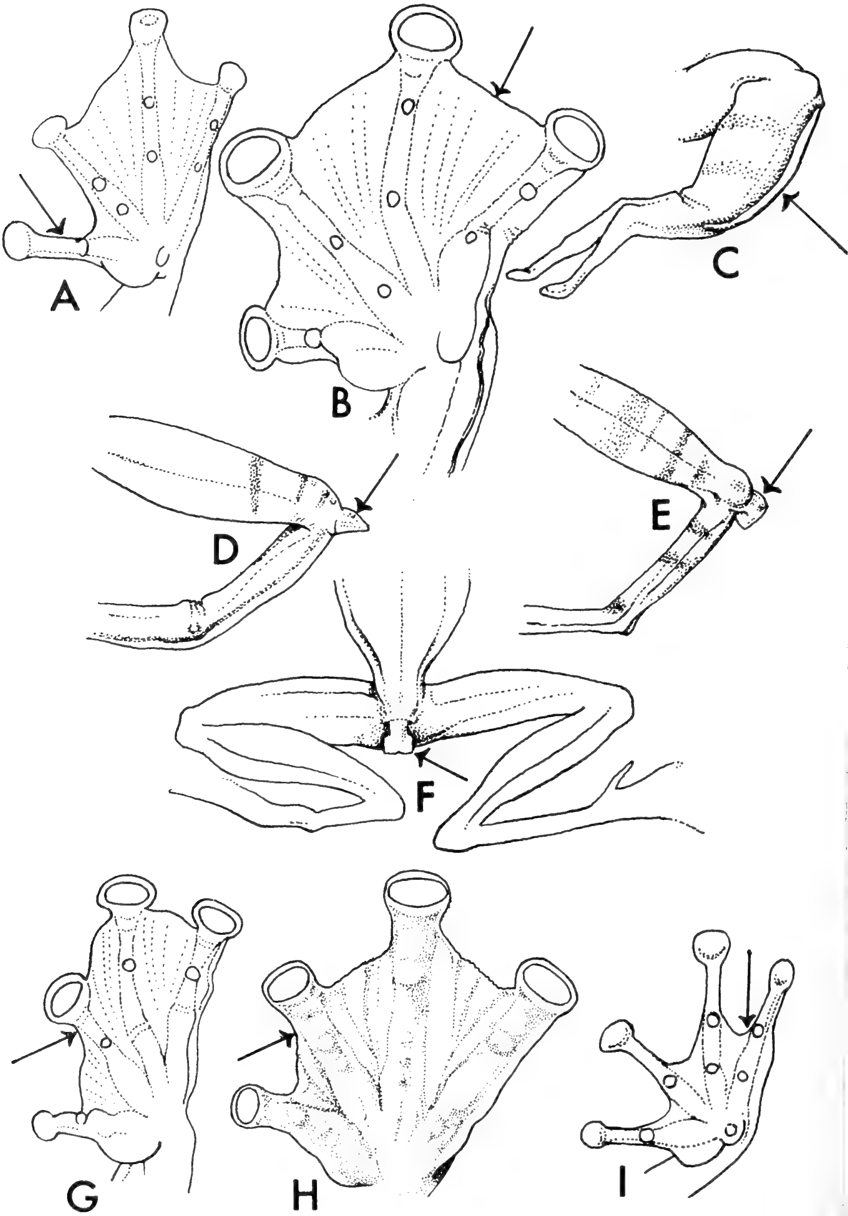


FIG. 55. Key to species of *Rhacophorus* from Borneo.

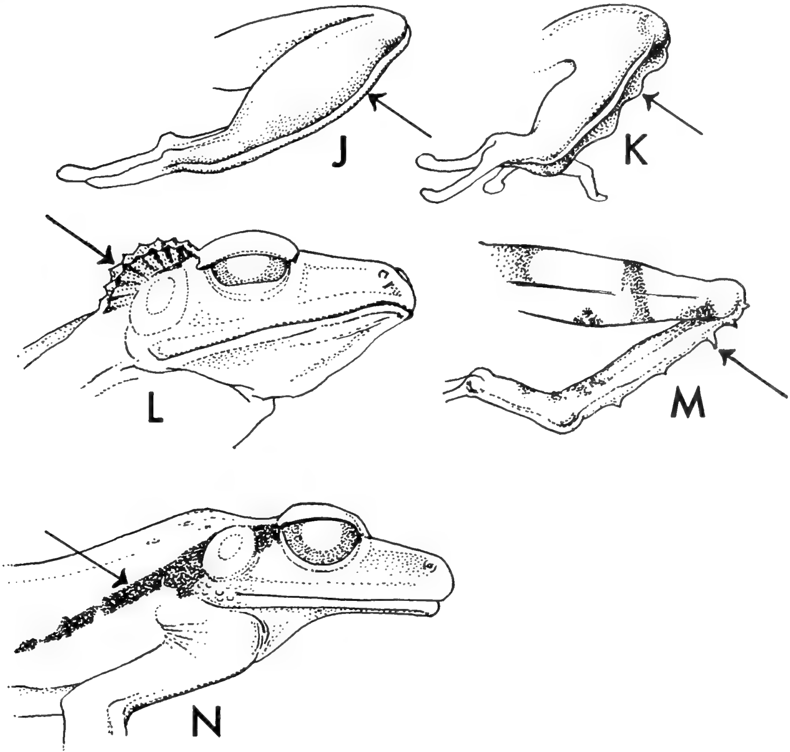


FIG. 55. (cont.) Key to species of *Rhacophorus*.

13A. A broad dark brown stripe from eye to beyond axilla, covering tympanum (fig. 55N) . . . . *macrotis*.
B. No such lateral stripe . . . . 14.

14A. Back with four dark longitudinal stripes . . . . *leucomystax*.
B. Back without longitudinal stripes . . . . 15.

15A. Small tubercles below eye and at rictus; a straight fold of skin from eye to behind level of axilla . . . . *colletti*.
B. No tubercle below eye; a sharply curved fold of skin from eye to axilla . . *hosei*.

KEY TO KNOWN LARVAE OF BORNEAN *Rhacophorus*.

(All in limb bud stages.)

1A. No beaks or expanded lips . . . . *hosei*.
B. Beaks and expanded lips present . . . . 2.

2A. Tail distinctly bicolored, dark behind vertical line at middle; labial teeth usually I:5–5/1–1:II . . . . *dulitensis*.
B. Tail not colored as in preceding . . . . 3.

3A. Entire tadpole dark purplish or black; yellowish spots on side of body and tail; labial teeth usually I:3–3/1–1:III . . . . larva B.

B. Coloration not as in preceding . . . . 4.

4A. Body pale gray or yellow, without markings; tail with bold black spots or mottling; labial teeth usually I:4–4/1–1:II . . . . *nigropalmatus.*

B. Coloration of tail not contrasting so sharply with that of body . . . . 5.

5A. Papillae continuous around border of lower lip; lower beak narrowly edged with black . . . . 6.

B. Papillae with distinct gap in center of lower lip; lower beak almost completely black (fig. 65) . . . . 9.

6A. Two outermost rows of teeth on upper lip continuous . . . . *pardalis.*

B. Only one continuous row of teeth on upper lip . . . . 7.

7A. Tail dark brown or black, with or without small light spots. . . . . 8.

B. Tail pale yellow with small dark spots . . . . *colletti.*

8A. Body dark, with light mottling; innermost row of teeth on lower lip narrowly interrupted . . . . *appendiculatus.*

B. Body dark, without light mottling; innermost row of teeth on lower lip continuous . . . . larva C.

9A. Both fins with a fleshy, opaque area in proximal third of tail (figs. 62 upper, 65) . . . . 10.

B. Fins without such opaque areas (fig. 62, lower) . . . . *leucomystax.*

10A. Innermost tooth row of lower lip narrowly interrupted (fig. 63) . . . . *macrotis.*

B. Innermost tooth row of lower lip continuous (fig. 65) . . . . *otilophus.*

Although the majority of species of *Rhacophorus* for which life histories are known have free-swimming, actively feeding tadpoles, some species have at least abbreviated this aquatic stage. Species such as *dulitensis, fasciatus, pardalis, leucomystax, otilophus,* and *macrotis* have larvae that hatch long before hind limb buds develop. In Philippine *leucomystax,* hind limb buds do not appear until eight to 14 days after hatching (Alcala, 1962). Tadpoles of *otilophus* and *macrotis* may not develop hind limb buds for several weeks after they begin to feed or not before their length is approximately twice that at hatching (Inger, 1956; *macrotis* is listed as *leucomystax linki* in that paper). Tadpoles of *dulitensis* may lack hind limb buds until they reach total lengths of 16 to 28 mm. (p. 297).

Yet within this series of species, trends toward lengthening the period of dependence on yolk, which is probably the first step toward direct development, are evident. At the time of hatching, larvae of *macrotis, leucomystax,* and *otilophus* have external gills and oral suckers. One day after hatching larval *macrotis* have the operculum closed and the gut coiled. In *leucomystax* the operculum closes and the gut coils on the second day after hatching. In larval *otilophus* the operculum closes on the third day and the gut coils on the fourth

day. Data on *leucomystax* are from Alcala (1962); those on *otilophus* and *macrotis* are from the egg masses reported by Inger (1956).

The larvae of *Rhacophorus hosei* (p. 306) have hind limb buds when about 12 to 15 mm. long. The complete absence of coiling in the gut at this stage suggests that the larvae subsist solely on yolk. The absence of horny beaks, expanded lips, gills, and operculum is indication of additional steps towards direct development.

Kirtsinghe (1946) recorded direct development of larvae he assigned to *Rhacophorus reticulatus* (= *R. microtympanum*). These Ceylonese larvae, which in terms of hind limb development were approximately in Stage XV, lacked beaks and oral disks but did have gills and opercula. Thus, though *microtympanum* and *hosei* abbreviate or eliminate the aquatic phase of larval life, they apparently have not followed identical paths of modification.

Rhacophorus acutirostris Mocquard

Rhacophorus acutirostris Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 151, pl. 11, fig. 1—Kina Balu, Sabah; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 260.

Rhacophorus angulirostris Ahl, 1927, Sitzber. Ges. Naturf. Fr. Berlin, **1927**, p. 45 (new name).

Rhacophorus schlegeli angulirostris Wolf, 1936, Bull. Raffles Mus., no. 12, p. 189.

Material examined.—Borneo 14 (5 BM; 6 MCZ; 3 MHNP, types of *acutirostris*); Sumatra 4 (NHMW).

Taxonomic notes.—Wolf (1936) placed three geographically isolated groups of forms into one wide-ranging species, *schlegeli*. The forms inhabiting Formosa, Riu Kiu Islands, and Japan (*moltrechti*, *owstoni*, *viridis*, and *schlegeli*) undoubtedly constitute a natural group that may be considered one species. The forms from southwestern China and those from the Sunda Islands are too distinct morphologically and too isolated geographically to be placed in the species *schlegeli*.

Description.—Size small, females 45–50 mm., males smaller; body robust, limbs slender; head usually broader than long, pointed; snout projecting, angular in profile, sloping forward from nostrils, then backward to mouth; nostril closer to tip of snout than to eye; canthus sharp; lores vertical, weakly concave; eye diameter longer than eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, about half eye diameter, 0.036–0.061 (median 0.048; N = 11) of snout-vent; vomerine teeth in widely separated, short, oblique groups that are narrowly separated from choanae.

Tips of fingers dilated into large, round disks, that of third finger usually wider than tympanum; web between first two fingers narrowly reaching subarticular tubercles of both fingers; outer edge of second finger broadly webbed to just beyond tubercle; third finger broadly webbed to basal tubercle on inner edge and to just beyond distal tubercle on outer edge; fourth finger broadly webbed to just beyond distal tubercle; a narrow fringe of skin on outer edge of fourth finger; supernumerary tubercles usually present on metacarpals. Tips of toes not as strongly dilated as outer fingers; first three toes broadly webbed to bases of disks or not so far on outer edges only, fifth toe similarly webbed on inner edge; fourth toe webbed to distal subarticular tubercle or slightly beyond on outer edge; two phalanges of second and third toes free of web on inner edges; a weak fringe of skin on outer edge of fifth toe; a small, oval, inner metatarsal tubercle, but no outer one; tibia 0.48–0.56 of snout-vent (median 0.505; $N = 9$).

Skin smooth above, coarsely granular below except on throat; a curved supratympanic fold from eye to axilla; skin free of skull; two or three low, whitish tubercles on outer edge of forearm; otherwise without dermal appendages.

Color (in alcohol) gray or brown above, lores often darker; a few individuals with white spot below eye; a narrow dark interorbital bar usually present; a dark X mark or short transverse bars sometimes visible on back; crossbars of limbs obscure; sides and rear of thighs with large, dark brown spots; below yellowish white, usually with many small dark spots.

Secondary sex characters.—Ten Bornean females measure 45.0–50.6 mm. (mean 47.89 ± 0.56); only two (45.9 and 47.9 mm.) contain enlarged ova. Three males with vocal sacs measure 32.3–33.1 mm. (mean 32.7). The median subgular vocal sacs have large oval openings near the corners of the mouth. None of these males has nuptial pads, but broad lineae masculinae are present at dorsal and ventral borders of the obliquus muscle.

Ecological notes.—Bornean specimens have been collected only on the massif of Kina Balu between 900 and 1300 meters above sea level. The Sumatran specimens listed above are from Padang on the mountainous western coast and, hence, may have been collected at elevations similar to those of the Bornean frogs.

Geographical variation.—The Sumatran frogs are identical to the Bornean ones in the characters studied.

Range.—Borneo and Sumatra.

SABAH: Kota Belud District, Kenokok, Kiau, and Luidan River, all on Mount Kina Balu.

Rhacophorus appendiculatus (Günther)

Polypedates appendiculatus Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 79—Philippine Islands.

Rhacophorus appendiculatus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 86, pl. 8, fig. 4; Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 150; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 255.

Rhacophorus appendiculatus appendiculatus Wolf, 1936, Bull. Raffles Mus., no. 12, p. 161; Inger, 1954, Fieldiana, Zool., **33**, p. 374; 1956, *ibid.*, **34**, p. 422.

Rhacophorus chaseni Smith, 1924, Proc. Zool. Soc. London, **1924**, p. 226, pl. 1, fig. 1—Teku River, Malay Peninsula.

Rhacophorus appendiculatus chaseni Smith, 1930, Bull. Raffles Mus., no. 3, p. 113.

Material examined.—Borneo 183 (160 FMNH; 1 NHMW; 3 RMNH; 19 SM); Sumatra 3 (1 ZMA; 2 ZMH); Mindanao 29 (11 CAS; 8 FMNH; 9 UMMZ; 1 USNM); Basilan 12 (5 CAS; 7 MCZ).

Taxonomic notes.—According to the original description of *Rhacophorus verrucosus* (Boulenger, 1893B), which Wolf considered to be a subspecies of *appendiculatus*, it has much less webbing between the fingers than *appendiculatus*, tubercles instead of a fringe below the vent, a different type of dermal appendage along forearm and tibia, and no rostral projection. Its relationship to *appendiculatus* is still uncertain.

Rhacophorus chaseni Smith is not sufficiently distinct from Philippine *appendiculatus* to warrant its recognition as a subspecies (see *Geographic variation* below).

Description.—Size small, females 45–50 mm., males smaller; body robust; limbs slender; head longer than broad; snout with a distinct conical projection (sometimes damaged in preserved material), angular in profile; nostril closer to tip of snout than to eye; canthus rounded; lores oblique; eye larger than eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, about one-half eye diameter; vomerine teeth in short, oblique groups beginning at anteromedial corners of choanae, groups widely separated.

Tips of fingers dilated into round disks having circummarginal grooves; width of largest disk about three-fourths tympanum diameter; web between first two fingers reaching subarticular tubercles as narrow fringe; web between third and fourth fingers reaching proximal or distal edge of outer subarticular tubercles; only one sub-

articular tubercle on fourth finger, tubercle with a longitudinal groove on distal half; no supernumerary metacarpal tubercles. Tips of toes with disks smaller than those of outer fingers; web reaching between subarticular tubercle and disk or to disk of first toe, to base of disk on outer edges of second and third toes and on inner edge of fifth, to between distal subarticular tubercle and disk or to disk on outer edge of fourth toe; an oval inner but no outer metatarsal tubercle; tibia 0.45–0.57 of snout-vent.

Skin above usually with irregular, low, thin intersecting ridges; a supratympanic fold from eye to axilla; skin free of skull; outer edge of forearm and fourth finger with continuous, crenulated fringe of skin; a similar fringe along tarsus; a narrow flap at heel; a transverse crenulate dermal projection below vent.

Color grayish brown above with dark, obscure mottling; limbs spotted, uniform, or barred, often with light areas at the elbows and heels; ventral surfaces cream-colored, without spots.

Secondary sex characters.—The adult Bornean females seen vary in snout-vent length from 42.4 to 50.1 mm. Adult males from Borneo vary between 29.6 and 37.0 mm. (see below, *Geographic variation*).

A yellowish nuptial pad occupies the dorsomedial edge of the first finger from the wrist to the level of the distal edge of the subarticular tubercle. Males also have median subgular vocal sacs. Lineae masculinae are absent.

Larvae.—A series of tadpoles was collected in a small, temporary pond. When the tadpoles were found, their beaks were visible but lacked horny covering; labial teeth were not evident; the gut was not coiled. Several were preserved on that date and others reared in the laboratory. Two preserved in Stages XI–XIV have dextral vents which do not reach the edge of the ventral fin and sinistral spiracles, characters that clearly identify them as *Rhacophorus* or *Philautus*. Two preserved in metamorphic stages have expanded disks on the fingers and toes, the toes incompletely webbed, and the fingers webbed to the subarticular tubercles. They also have light areas at the heels and elbows such as are found often in adults of *Rhacophorus appendiculatus*. They do not have dermal fringes along the limbs as do adult *appendiculatus*.

Despite this difference from adult *appendiculatus*, this developmental series is tentatively assigned to that species because the webbing of hands and feet is too extensive for some other species (e.g., *R. colletti*, *R. everetti*, and *R. hosei*) but not extensive enough for others (e.g., *R. fasciatus*, *R. harrissoni*, and *R. nigropalmatus*).

The following description is based on four tadpoles, Stages XI–XIX.

Body oval, slightly depressed; eyes dorsal, not visible from below; diameter of eye equal to eye-nostril distance, subequal to internarial distance, about three-fifths of interorbital width; spiracle sinistral below line connecting eye and base of hind limb, equidistant between eye and hind limb; anus dextral, opening not reaching margin of ventral fin.

Mouth ventral; beaks black-edged, finely serrate, upper beak concave; papillae small, in a continuous double row across lower lip; labial teeth I:3–3/1–1:II in all four tadpoles.

Total length 17.5–25 mm.; tail 0.63–0.66 of total length, margins convex; dorsal fin rising in middle third of tail length; tail abruptly narrowed near end to a drawn-out, blunt tip; caudal muscle not as deep as fins.

Color of head, body and tail dark brown; rear of body with obscure light mottling; caudal muscle with light spots; fins dusky; base of tail without thickened opaque area.

Ecological notes.—Bornean specimens have been caught in primary hill forest (29), in primary swamp forest (70), and in secondary growth in swampy areas (55). Almost all were perched on low vegetation one or two meters above ground. One frog was caught 21 meters above ground. The majority are from localities within 50 meters of sea level; 25 are from a hill forest 500 meters above sea level.

Larvae were found in a pool formed by flood waters in a swamp forest.

Calling males have been collected in June, July, August, October, and November. The larvae were obtained in December. Probably breeding occurs in most months of the year.

Geographic variation.—A slight amount of variation occurs in the extent of web in the Bornean samples (Table 36). The first toe may be fully webbed to the disk, to the subarticular tubercle only, or mid-way between these points. Frogs from the headwaters of the Baleh River in central Sarawak have full webbing extending to the disk, whereas those from Niah in northern Sarawak and from Sandakan in eastern Sabah usually have the full web ending between the tubercle and the end of the disk. The web between the third and fourth fingers is full to the distal edge of the outer subarticular tubercle of the fourth finger or beyond in the Baleh series, but in the other Bornean specimens usually is full only as far as the proximal edge of the tubercle.

TABLE 36.—Frequency distribution in extent of web in *Rhacophorus appendiculatus*.

	Web of first toe[1]		
	To disk	Mid-way	To tubercle
Bornean samples:			
Baleh River	25	0	0
Niah	5	10	0
Sandakan	4	11	1
Philippine samples:			
Mindanao	0	14	2
Basilan	0	5	1

	Web between third and fourth fingers[1]		
	Distal edge of tubercle	Base of tubercle	Not reaching tubercle
Bornean samples:			
Baleh River	25	0	0
Niah	2	13	0
Sandakan	3	13	0
Philippine samples:			
Mindanao	0	5	11
Basilan	0	0	6

[1] For explanation of categories see text.

Although all Bornean specimens have crenulated fringes along the lower arm and tarsus, these appendages are distinctly wider in the Baleh River series.

The Baleh specimens also have slightly longer legs than the other Bornean ones. The tibia ratios (in thousandths of snout-vent) in adult males of the Bornean samples are: Baleh River 511–571 (median = 534; N = 20), Niah 465–533 (median = 501; N = 9), Sandakan 451–537 (median = 512; N = 15). The null hypothesis of no difference among these samples must be rejected; H (of Kruskal-Wallis test) equals 23.21, equivalent to $P < 0.001$. Adult males (with vocal sacs and nuptial pads) from the three Bornean samples differ in size. Those from Sandakan measure 29.6–34.1 mm. (mean 31.81 ± 0.26; N = 15), those from Niah 32.8–37.0 (mean 34.95 ± 0.32; N = 14), and those from the upper Baleh 33.2–37.0 (mean 35.27 ± 0.22; N = 24). The differences between the Sandakan males and the others are statistically significant ($t > 7.0$; $P < 0.001$).

Philippine specimens have less extensive webbing than the Bornean ones (Table 36). As has been observed (Smith, 1930; Inger, 1954A), the dermal appendages of the limbs and body of Philippine

frogs are narrower than those of Bornean ones. The edges of the fringes on the limbs are smooth in Philippine frogs, crenulate in Bornean ones. Because the differences in webbing and dermal appendages are parallel and because both characters involve the same kind of tissue, it is conceivable that a single gene change could account for both differences and that only a single morphogenetic change is involved. To recognize the subspecies *chaseni* on such a basis would be in effect to base a subspecies on a single character that is conspicuous to the taxonomist's eye.

Two of the three Sumatran specimens seen resemble the Bornean population in the development of cutaneous appendages; the third one has narrow, smooth-edged fringes as in the Philippine frogs.

Range.—Malay Peninsula (Smith, 1930), Sumatra, Borneo, and the Philippine Islands.

SABAH: Kinabatangan District, Deramakot; Sandakan District, 8 miles north of Sandakan; Tawau District, Kalabakan. SARAWAK: Third Division, Mount Dulit (van Kampen, 1923), Menuang (headwaters of Baleh River); Fourth Division, Baram River, Labang, Niah, Nyabau. KALIMANTAN: Merah, Sintang.

Rhacophorus baluensis Inger

Rhacophorus baluensis Inger, 1954, Jour. Washington Acad. Sci., 44, p. 250—Bundu Tuhan, Mount Kina Balu, Sabah.

Material examined.—Borneo 3 (1 FMNH, paratype; 2 USNM, holotype and paratype).

Description.—A medium-sized species, females 60–65 mm., males about 55 mm.; body and legs moderately robust; head as long as broad, 0.36 of snout-vent; snout pointed, projecting; nostril about twice as far from eye as from tip of snout; canthus sharp; lores oblique, feebly concave; eye diameter slightly longer than eye-nostril distance; interorbital wider than eyelid; tympanum distinct, about three-fifths eye diameter, about 0.067 of snout-vent; vomerine teeth in long, oblique groups beginning near anterior corners of choanae, groups separated by more than half length of one group.

Tips of fingers expanded into large disks, that of third finger wider than tympanum and 0.08 (1 measured) of snout-vent; broad web to center or distal edge of subarticular tubercles on first finger and inner side of second, to base of disk on outer edge of second, to outer subarticular tubercle on inner edge of third, to bases of disks or not quite so far on outer edge of third and inner edge of fourth fingers; a narrow fringe of skin on outer edge of fourth finger; a supernumerary

tubercle on each metacarpal. Tips of toes with disks smaller than those of fingers; broad web to base of disks on outer edges of first three toes and inner edge of fifth, to distal edge of outer subarticular tubercle on both sides of fourth toe; a narrow fringe of skin on outer edge of fifth toe; an oval inner but no outer metatarsal tubercle.

Skin smooth above, free of skull; a weakly curved fold from eye over tympanum to just beyond shoulder; throat rugose; abdomen coarsely granular; a narrow fringe of skin beginning above elbow continuous to fourth finger; a similar fringe along tarsus meeting that of fifth toe; a long, pointed dermal flap at heel; a narrow, curved, transverse ridge above vent.

Color (in alcohol) above grayish brown with numerous dark, transverse bars or obscure dark spots; sides and rear of thighs with small white spots; limbs with dark crossbars; ventral surfaces whitish; a few dark spots on throat; ridge above vent white with a narrow black edge.

Secondary sex characters.—The single adult male has slit-like vocal sac openings at the sides of the mouth and a gray nuptial pad on the dorsomedial surface of the first finger. The male is 54 mm.; the two females 61 and 64 mm.

Ecological notes.—The three known specimens were caught at 1375 meters above sea level.

Range.—Sabah.

SABAH: Ranau District, Bundu Tuhan on Mount Kina Balu.

Rhacophorus colletti Boulenger. Figure 56.

Rhacophorus colletti Boulenger, 1890, Proc. Zool. Soc. London, **1890**, p. 36—Langkat, Sumatra; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 250.

Rhacophorus cruciger (nec Blyth) Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, p. 150.

Rhacophorus leucomystax leucomystax Wolf, 1936, Bull. Raffles Mus., no. 12, p. 178.

Material examined.—Borneo 41+larvae (1 ANSP; 3 BM; 36+larvae FMNH; 1 SM); Rhio Archipelago 1 (USNM); Lingga Islands 1 (USNM); Great Natuna Island 1 (BM).

Taxonomic notes.—This species differs from *leucomystax* in having a much more pointed snout, longer legs (tibia 0.56–0.66 of snout-vent, 0.47–0.60 in *leucomystax*), wider finger tips (disk of third finger 0.061–0.084 of snout-vent, 0.041–0.059 in *leucomystax*), a conical or triangular dermal appendage at the heel, and the skin free of the

FIG. 56. *Rhacophorus colletti*, 80 mm.

skull even in adult females (up to 75 mm.). The range of *colletti* overlaps that of *leucomystax* from the Malay Peninsula (Smith, 1930) and Sumatra to eastern Sabah. Under these circumstances, Wolf's placing *colletti* in the synonymy of *leucomystax* (Wolf, 1936) was a serious error.

Description.—Size small to moderate, males to 52 mm., females to 78 mm.; body and legs slender; head triangular, longer than broad; length 0.36–0.41 of snout-vent, width 0.33–0.38; snout acutely pointed, strongly projecting; nostril twice as far from eye as from tip of snout, over tip of mandible; canthus sharp; lores oblique, not concave; eye equals eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, two-thirds to three-fourths eye diameter; vomerine teeth in long oblique groups beginning at anterior corners of choanae, groups separated by less than length of one.

Tips of fingers dilated into large disks; width of largest disk about two-thirds diameter of tympanum; fingers without web; a conspicuous supernumerary tubercle on each metacarpal. Tips of toes not as widely dilated as those of fingers; broad web reaching base of disk or not quite so far on outer edges of first three toes and on inner edge of fifth; fourth toe usually with a broad web only to distal subarticular tubercle on outer edge and not so far on inner edge; a small oval, inner metatarsal tubercle, but no outer one; tibia 0.56–0.66 of snout-vent (median 0.618; N = 11).

Skin shagreened above, coarsely granular below; low tubercles around eye and at rictus; a narrow horizontal fold from eye, passing above tympanum, and ending behind axilla; skin of head free of skull; outer edge of forearm with very low, whitish tubercles; a small conical dermal appendage at heel; no other dermal appendages.

Color grayish or reddish brown above, whitish below; usually a solid, dark hour-glass figure beginning at interorbital and ending at sacrum; a dark line from each posterior corner of figure to groin; legs with dark crossbars.

Secondary sex characters.—Five females measure 59.3–77.3 mm. (mean 68.2) and six males 44.0–51.8 mm. (mean 48.5). The sexes do not differ in relative head length, head width, tympanum diameter, or tibia length.

Males have paired subgular vocal sacs with openings at the corners of the mouth. The yellowish nuptial pad covers the dorsomedian edge of the first finger from the wrist to above the subarticular tubercle. A pink linea masculina is present only at the ventral border of the obliquus muscle.

Larvae.—A group of tadpoles was reared in the field laboratory until one erupted the fore limbs. In the pre-metamorphic larvae the papillae of the upper lip are confined to the corners, the spiracle is sinistral and the vent dextral, the opening not reaching the margin of the ventral fin. They are therefore rhacophorid larvae.

The metamorphosing froglet (Stage XX) has no webbing between the fingers and no fringes of skin along the lower arm. The second finger is only slightly longer than the first and is about half as long as the third. The tip of the second finger does not reach the distal subarticular tubercle of the third finger. The only Bornean rhacophorid having this combination of characters is *Rhacophorus colletti*.

The following description is based on four pre-metamorphic larvae.

Body oval, very slightly depressed; eyes dorsal, not visible from below; eye equal to eye-nostril distance, half of interorbital width; spiracle sinistral, in line between eye and root of hind limb, closer to eye; anus dextral, opening not reaching margin of fin.

Mouth ventral, subterminal, beaks black-edged, finely serrate; upper beak a smooth arc; papillae small, homogeneous, in a continuous double row along lower lip, confined to corners of upper lip; teeth on upper lip I:3–3 in two pre-limb bud tadpoles, I:4–4 in two older ones (Stages VII and IX); teeth of lower lip 1–1:II in all four, the innermost row only narrowly interrupted.

Tail 0.59–0.66 of total length, moderately convex, tapering abruptly before end to form a drawn-out tip; fins deeper than caudal muscle beyond middle of tail.

Color pale yellow; head and body with large, faint dark spots; tail with smaller black spots; a pigmentless band dorsally across root of tail.

Total length of pre-limb bud stage 16 mm., of Stage VII 22 mm., of Stage XX 22 mm. Snout-vent of last 9 mm.

Ecological notes.—Most of the Bornean specimens have been collected in flat areas close to the coast. All have been caught within 200 meters of sea level.

Those for which data are available were found in primary forest (14) or in logged, marshy forests (13); all were perched on vegetation 0.6–6 mm. above the ground. The series of tadpoles was collected from a small pool left by receding flood waters in swamp forest.

Range.—Extreme southern, peninsular Thailand (Smith, 1930), Sumatra, Borneo, and islands of the South China Sea.

SABAH: Beaufort District, Lambidan; Labuk District, Paitan; Sandakan District, Sandakan. SARAWAK: First Division, Bako National Park; Fourth Division, Marudi, Niah, Nyabau, Labang, Sungei Pesu.

Rhacophorus dulitensis Boulenger. Figure 57.

Rhacophorus dulitensis Boulenger, 1892, Proc. Zool. Soc. London, **1892**, p. 507, pl. 30, fig. 1—Mount Dulit, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 258; Wolf, 1936, Bull. Raffles Mus., no. 12, p. 210 (part).

Rhacophorus chiropterus Werner, 1896, Verh. Zool. Bot. Ges. Wien, **46**, p. 22, pl. 1, fig. 2—"North Borneo."

Material examined.—Borneo 4+larvae (2 BM, including type of *dulitensis*; 1+larvae FMNH; 1 ZMB, type of *chiropterus*); Sumatra 8 (1 MCZ; 6 RMNH; 1 ZMA).

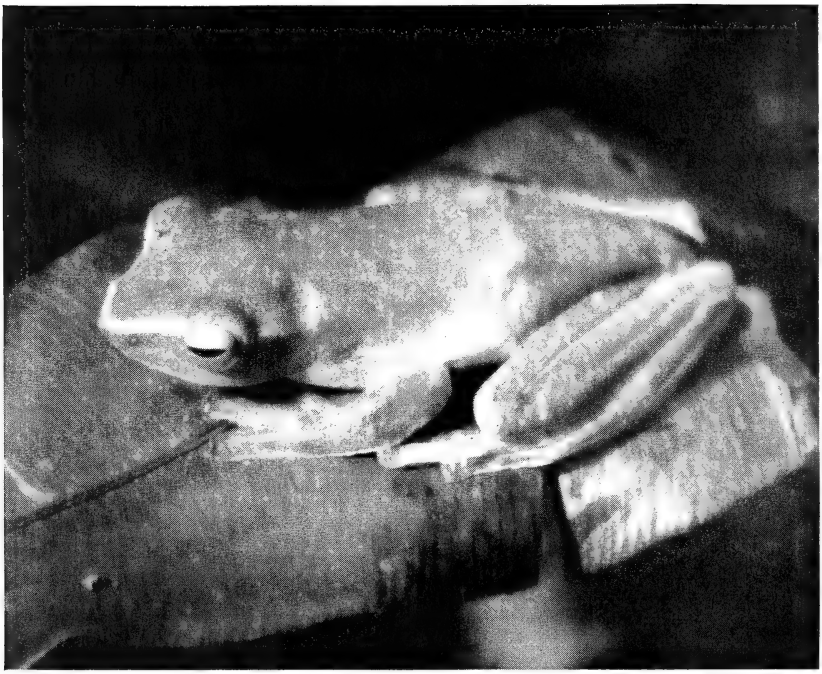


FIG. 57. *Rhacophorus dulitensis*, 49 mm.

Taxonomic notes.—Wolf (1936) treated *Rhacophorus bimaculatus* Boulenger (= *Rhacophorus bipunctatus* Ahl) as a subspecies of *reinwardti*. Actually, *bimaculatus* is more similar to *dulitensis* in size, head shape, webbing of the fingers, and dermal appendages than to *reinwardti*. Wolf's key (p. 154) is misleading in stating that *reinwardti* has no projecting anal appendage; the types and four of the other six Javan frogs I have seen have strongly projecting, wide flaps over the vent. It thus does not differ from *dulitensis* in the presence or absence of this structure.

Rhacophorus dulitensis has a ridge, narrower than the width of a finger, along the outer edge of the forearm; *reinwardti* has at that position a flap greater in width than a finger. In *dulitensis* the web as a broad sheet reaches the base of the disk on the outer edge of the third finger but not on the inner edge. In *reinwardti* the web is full to the disk on both sides of the third finger and on the outer edge of the second as well. The head is longer than wide in *dulitensis* but as wide as or wider than long in *reinwardti*. *Rhacophorus bimaculatus* (7 examined) agrees with *dulitensis* and differs from *reinwardti* in

these characters. The first two species are smaller (mature males 33–36 mm. in *dulitensis*, 34–38 in *bimaculatus*) than *reinwardti* (mature males 46–55 mm.).

In one respect *bimaculatus* resembles *reinwardti*: five of the *bimaculatus* seen have a small black spot on the dorsal surface of the web between the two outer toes. The pigmented area, however, is not as large as it is in any of the *reinwardti* examined. No *dulitensis* has similar spots. *Rhacophorus bimaculatus* differs from Bornean *dulitensis* and *reinwardti* and resembles *prominanus* Smith and Sumatran *dulitensis* in having a pointed, projecting snout.

Rhacophorus prominanus Smith is the only one of the series having a supra-anal flap in which the end of the gut is itself involved in the anal appendage and projects beyond the thighs.

Of these four forms, *reinwardti* and *dulitensis* occur in Sumatra and are probably sympatric there; *prominanus* and *bimaculatus* are sympatric in northern Malaya. The finding of a typical specimen (MCZ 22776) of *prominanus* on Nias Island west of Sumatra indicates that the species probably occurs on Sumatra and that it is probably sympatric with *dulitensis*. All should be recognized as distinct species until such time as the gaps in distributions (e.g., southern Malaya, eastern Sumatra, and western Borneo) are closed and more specimens are known. They may be identified by the following key:

A transverse flap of skin projecting from body above vent; at least the fourth finger broadly webbed to the disk.

1A. Third finger broadly webbed to disk on both sides . . . . 2.
B. Third finger at most broadly webbed to disk on outer edge only . . . . . . 3.

2A. Vent in appendage projecting beyond thighs . . . . *prominanus* Smith.
B. Vent not projecting beyond thighs . . . . *reinwardti* Schlegel.

3A. One or more large, black, lateral spots, the first in axilla *bimaculatus* Boulenger.
B. Sides without large black spots . . . . *dulitensis* Boulenger.

Description.—Size small (to ca. 45 mm.); body and legs slender; head longer than broad, pointed; snout rounded or pointed in profile, slightly projecting; nostril closer to tip of snout than to eye; canthus sharp; lores vertical or nearly so, not concave; eye diameter greater than eye nostril distance; interorbital wider than upper eyelid; tympanum distinct, about two-thirds eye diameter; vomerine teeth in short transverse rows between anterior portions of choanae, distance between groups greater than length of one group, closer to choanae.

Tips of fingers dilated into broad disks, all of them narrower than tympanum; broad web to subarticular tubercles between first two

fingers, to disk on outer edge of second finger, to below disk on inner edge of third, to disk on outer edge of third and inner edge of fourth; no visible supernumerary metacarpal tubercles. Disks of toes distinct, but smaller than those of outer fingers; all toes webbed to disks (in Bornean specimens); an oval inner but no outer metatarsal tubercle; tibia 0.47–0.49 of snout-vent.

Skin smooth above; coarsely granular below; skin of head free of skull; no supratympanic fold; a narrow, white-edged ridge of skin along outer edge of forearm and tarsus; a small, conical or round flap at heel; smooth-edged or crenulate transverse fold of skin projecting above vent.

Color (in life) pea green above with fine white spots; a yellowish white canthal stripe; a reddish brown patch on each eyelid; concealed surfaces of limbs greenish yellow; webbing same color except between two outer toes where webbing is red; throat and chest white, abdomen green. In alcohol, pale yellowish above; a dark line below canthus; eyelids with purplish spot; limbs without crossbars; ventral surfaces cream colored; web without spots.

Secondary sex characters.—Males have subgular vocal sacs with round or long openings at the corners of the mouth. The yellowish nuptial pad covers the dorsal surface of the first finger from its base to the level of the subarticular tubercle. Males have numerous whitish spicules scattered over the entire dorsal surface and under the mandible. Six males with vocal sacs measure 32.6–35.5 mm. (mean 34.36 mm.). One dried female containing enlarged ova is about 35 mm. long.

Larvae.—Fourteen tadpoles ranging from pre-limb bud to pre-metamorphic stages of development have the characters of larval *Rhacophorus*: spiracle sinistral, vent dextral and not reaching margin of ventral fin, and papillae of upper lip confined to corners. The most advanced, a stage XIX tadpole, has characteristics of adult *R. dulitensis:* a transverse, horizontal projection above the anus; a narrow fringe of skin at the heel; and outer fingers broadly webbed beyond level of subarticular tubercles. The first character is diagnostic of *dulitensis*.

The following description is a composite based on the entire series.

Body ovate, flattened above and below; eyes dorsal, not visible from below; diameter of eye equal to eye-nostril distance, slightly less than internarial distance, and about one-half interorbital width; spiracle sinistral, non-tabular, below line connecting eye and root of

hind limb, much closer to eye than to hind limb bud; anus dextral, opening not reaching margin of fin.

Mouth ventral, subterminal; beaks black-edged, finely serrate, upper one a smooth arc; papillae small, homogeneous, in an uninterrupted double row across lower lip; papillae confined to lateral corners of upper lip; teeth of upper lip I:4–4 (2 specimens) or I:5–5 (9), those of lower lip 1–1:II (11).

Tail 0.59–0.64 of total length, moderately heavy, margins weakly convex, tapering abruptly near end to a drawn out, blunt tip, dorsal fin beginning at end of body; caudal muscle deeper than either fin in proximal half.

Color in life of head and body light grayish brown above, whitish below; body without pattern; tail pale grayish brown proximally; a black, wavy, vertical line at middle of tail; tail dark gray behind line.

Sizes at various stages are:

Stage	No.	Head-plus-body	Total
pre-limb bud	1	9.5	24
I	1	11.0	30
IV	1	16.0	41
X	1	17.0	43
XI	2	15.4–15.9	41
XIII	2	14.9–15.8	39–41
XIV	1	15.9	41
XVI	1	17.2	44
XVIII	3	15.3–16.3	40–43
XIX	1	16.9	42

Geographic variation.—The snout in Sumatran specimens is more pointed than in the Bornean frogs seen. The outer edge of the third finger is fully webbed to the disk in Bornean frogs, but not quite so far in the Sumatran series.

Range.—Sumatra and Borneo.

SABAH: Sandakan District, Sandakan. SARAWAK: Third Division, Mount Dulit, Mengiong River; Fourth Division, Baram (van Kampen, 1923), Niah.

Rhacophorus everetti Boulenger

Rhacophorus everetti Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**, p. 87—Palawan.

The Palawan frog, *everetti*, is so similar to the Bornean *macroscelis* that they must be considered conspecific. Besides being the only Indo-Malayan forms of *Rhacophorus* having rows of isolated, pointed tubercles on the tarsi, the two are alike in habitus and coloration.

Both have broad heads with pointed snouts and sloping lores, long legs, and a dark X- or H-shaped mark on the back.

They differ in minor ways. The Bornean form has longer tubercles than the Palawan one and has them on the dorsal surfaces of the head and body, which are smooth in Palawan specimens. The interorbital marking in *everetti* is a narrow dark bar; in *macroscelis* it is a broad dark area split by a narrow, light interorbital bar. The tympanum is slightly smaller in *everetti* (0.045–0.051 of snout-vent in 6; median 0.047) than in *macroscelis* (0.057–0.064 in 4; median 0.061).

Despite these differences, the two forms are much more similar to one another than either is to any other Indo-Malayan form. The close relationship of these allopatric frogs is best expressed by treating them as subspecies: *everetti everetti* Boulenger (range: Palawan), and *everetti macroscelis* Boulenger (range: Borneo).

Rhacophorus everetti macroscelis Boulenger

Rhacophorus macroscelis Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 403—Mount Kina Balu, Sabah; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 252; Smith, 1931, Bull. Raffles Mus., no. 5, p. 31.

Philautus spiculatus Smith, *ibid.*, p. 20, pl. 1, fig. 2—Kenokok, Mount Kina Balu, Sabah.

Rhacophorus spiculatus Inger, 1954, Jour. Washington Acad. Sci., **44**, p. 251.

Rhacophorus buergeri hosii (nec. Boulenger) Wolf, 1936, Bull. Raffles Mus., no. 12, p. 170.

Material examined.—Borneo 6 (2 BM, holotypes of *macroscelis* and *spiculatus*; 1 FMNH; 1 MCZ; 2 USNM).

Taxonomic notes.—Contrary to the implication in the original description of *Philautus spiculatus* (Smith, 1931A), vomerine teeth are present on one side in the holotype and in other specimens seen (Inger, 1954B). This common anomaly of the genus *Rhacophorus* (Inger, 1956, p. 410) accounts for Smith's error in associating *spiculatus* with *Philautus* instead of *Rhacophorus*.

Direct comparison of the holotypes of *macroscelis* and *spiculatus* removes all doubt as to their identity. Both have the row of long pointed tubercles along the tarsus, the rough skin of the dorsum, and the characteristic dark H-shaped mark on the back typical of the species.

The placing of *macroscelis* in the synonymy of *hosei* by Wolf (1936) is unwarranted and illustrates once more the basic defect of Wolf's monograph—a failure to understand the nature of individual and interspecific variation in the genus *Rhacophorus*. The holotype

of *hosei* has been examined in the course of this study, and by no stretch of imagination can the differences between it and *macroscelis* be considered individual variation because of the constancy of other specimens of *macroscelis* and *hosei* in the characters (size, habitus, skin ornamentation, pattern, etc.) distinguishing them.

Description.—Size small, females to 50 mm., males smaller; body robust; legs long; head large, wider than long, width 0.38–0.45 of snout-vent, length 0.36–0.42; snout pointed, projecting; nostril much closer to tip of snout than to eye, in a small prominence; canthus sharp, curved; lores concave, sloping; eye diameter slightly longer than eye-nostril distance; interorbital wider than upper eyelid, tympanum distinct, about half eye diameter, 0.057–0.064 of snout-vent; vomerine teeth usually present in short, oblique groups beginning at or close to anteromedian corners of choanae, distance between groups usually greater than width of a group.

Tips of fingers dilated into large, round disks, that of third finger wider than tympanum; fingers narrowly webbed at bases; obscure supernumerary metacarpal tubercles present or not. Tips of toes slightly narrower than those of fingers; broad web reaching subarticular tubercle of first toe, almost to base of disk on outer edge and to subarticular tubercle on inner edge of second toe, midway between the two tubercles on the inner edge and to between distal tubercle and disk or to base of disk on outer edge of third toe, to distal tubercle of fourth toe or not so far on both sides of fourth toe, and to base of disk on fifth toe; a smaller inner, but no outer metatarsal tubercle.

Skin of back shagreened and usually with pointed tubercles that are especially conspicuous on forehead and eyelid; skin of head free of skull; sides and entire ventral surface coarsely granular; two to four long, pointed tubercles on outer edge of forearm; similar tubercles on tarsus, beginning at heel and usually extending along edge of fifth metatarsal; two or more long, white tubercles below vent.

Color (in alcohol) yellowish brown; a large dark brown spot on forehead split by a narrow, light interorbital bar; a dark stripe from tip of snout to eye just below canthus; a dark spot below anterior half of eye, another running down to lip from rear corner of eye, and a third from eye across tympanum; a dark X or H-shaped mark on back, beginning at upper eyelids and ending on sacrum; rest of back and sides with irregular dark markings; limbs with dark crossbars; below cream-colored with or without small dark spots.

Secondary sex characters.—Two adult females measure 46.8 and 48.8 mm. The only male known, the holotype of *macroscelis*, is 30.2

mm. It has a yellowish nuptial pad dorsomedially on the first finger, from the base of the finger to the level of the subarticular tubercle.

Ecological notes.—This species has been collected so far only on the massif of Kina Balu between elevations of 900 and 1375 meters.

Range.—Northwestern Borneo.

SABAH: Kota Belud District, Kenokok, Kiau; Ranau District, Bundu Tuhan.

Rhacophorus fasciatus Boulenger

Rhacophorus fasciatus Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **16**, p. 169—Akah River, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 262; Wolf, 1936, Bull. Raffles Mus., no. 12, p. 209.

Rhacophorus shelfordi Boulenger, 1900, Proc. Zool. Soc. London, **1900**, p. 185, pl. 17, fig. 2—Mount Penrissen, Sarawak; van Kampen, *op. cit.*, p. 262; Smith, 1925, Sarawak Mus. Jour., **3**, p. 34.

Material examined.—Borneo 6 (3 BM, holotype of *shelfordi*, syntypes of *fasciatus;* 1 FMNH; 2 RMNH).

Taxonomic notes.—As the types of *shelfordi* and *fasciatus* differ only in color pattern (*shelfordi* with anterior transverse bars fused to form a cross; *fasciatus* with transverse bars only), Wolf (1936) is correct to synonymize them. The types agree in habitus, webbing, body proportions, and absence of dermal appendages.

Description.—Small (males 40–45 mm.) to moderate (females 50–55 mm.) in size; body slender to moderately robust; legs slender; head triangular, length 0.36–0.37 of snout-vent, width 0.35–0.36; snout obtusely pointed, projecting slightly; nostril centered between eye and tip of snout or a little closer to latter; canthus sharp; lores slightly oblique, not concave; eye diameter much longer than eye-nostril, three-fourths to four-fifths length of snout; interorbital wider than eyelid; tympanum distinct, about two-thirds eye diameter, 0.069–0.074 (2 measured) of snout-vent; vomerine teeth in long, transverse or oblique groups beginning near anterior corners of choanae, groups separated by less than half length of one group.

Tips of fingers dilated into large disks, that of third finger not as wide as tympanum and about 0.06 of snout-vent; broad web reaching base or center of subarticular tubercle of first finger, distal margin of tubercle on inner edge of second finger, and to bases of disks on outer edge of second, both sides of third, and inner edge of fourth finger; a wide fringe of skin on outer edge of fourth finger; a supernumerary tubercle on each metacarpal. Tips of toes expanded into disks smaller than those of fingers; all toes webbed to disks; narrow

fringes of skin along inner edge of first toe and outer edge of fifth; a small inner, but no outer metatarsal tubercle; tibia 0.51–0.54 of snout-vent.

Skin smooth above, free of skull; a straight fold from eye above tympanum, ending at shoulder; skin of throat smooth in females, rugose in males, abdomen coarsely granular; no ridges or flaps of skin on arms, legs, or at vent; a row of weak tubercles on lower arm.

Color (in alcohol) brownish or grayish above; narrow interorbital and prefrontal bars; back with transverse dark bars or spots; ventrally cream colored, usually with small brown spots; limbs with dark crossbars.

Secondary sex characters.—Four males with vocal sacs measure 38.1–44.5 mm. The only female with enlarged ova is 52.5 mm. The vocal sac openings are round and situated at the corners of the mouth. The yellowish nuptial pad covers a small dorsomedial area on the first finger from its base to the level of the subarticular tubercle. Lineae masculinae are absent.

Ecological notes.—One adult male was caught after it leaped from an epiphyte 5 m. above the ground in primary rain forest.

Range.—Borneo.

SARAWAK: First Division, Mount Penrissen; Fourth Division, Akah River, Sungei Pesu. KALIMANTAN: Balikpapan.

Rhacophorus harrissoni Inger and Haile. Figure 58.

Rhacophorus harrissoni Inger and Haile, 1959, Sarawak Mus. Jour., **9**, p. 270, figs. 1–2—Ulu Patah, Baram basin, Sarawak.

Material examined.—Borneo 25 (23 FMNH, including holotype; 1 NHMW; 1 RMNH).

Taxonomic notes.—Following publication of the original description, I examined the types of *shelfordi* Boulenger and *fasciatus* Boulenger. The differences noted earlier (Inger and Haile, 1959) between *harrissoni*, on the one hand, and *fasciatus* and *shelfordi*, on the other, are confirmed. The specimens of *harrissoni* differ further from Boulenger's forms in having more extensively webbed fingers. In *harrissoni* broad webbing reaches the distal edge of the subarticular tubercle of the first finger and the base of the disk on the inner edge of the second; in the types of *fasciatus* and *shelfordi* broad webbing reaches the base of the tubercle of the first finger and extends just beyond the tubercle on the inner edge of the second finger.

Adult males of *harrissoni* have sharply pointed snouts projecting beyond the mandible for a distance equal to half the diameter of the

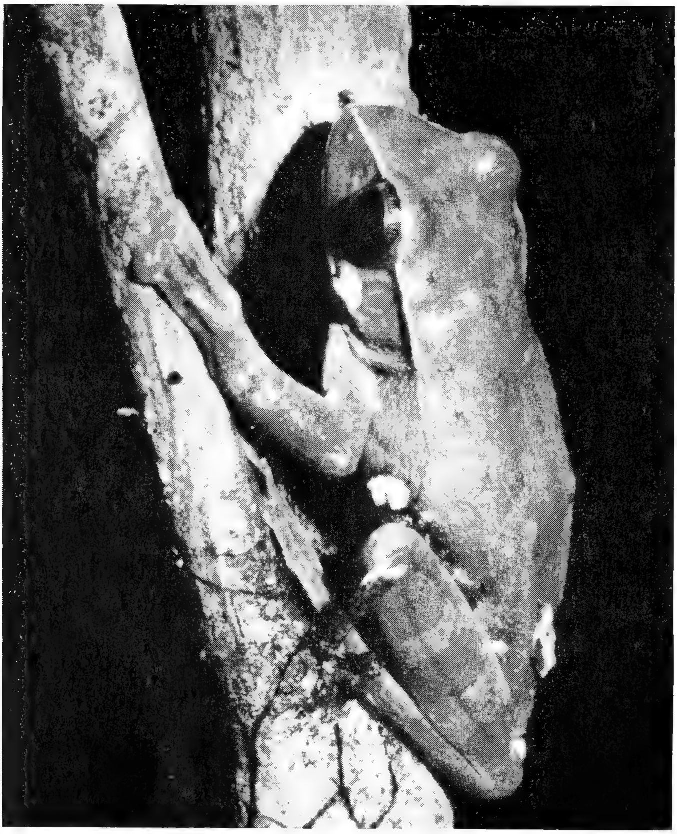


FIG. 58. *Rhacophorus harrissoni*, adult female, 70 mm.

tympanum. Adult males of *fasciatus*, however, have obtusely pointed snouts that project beyond the mandible for a distance equal to but a third of the diameter of the tympanum.

Rhacophorus harrissoni also appears to be larger than *fasciatus* (cf. sizes given in *Secondary sex characters*).

Description.—A moderate-sized species, adult females to 70 mm., males to 55 mm.; body and legs robust; head triangular, usually longer than broad, length 0.36–0.37 of snout-vent, width 0.33–0.37; snout obtusely pointed, projecting (see *Secondary sex characters*); nostril nearer tip of snout than to eye, but not twice as far from eye as from snout; canthus sharp; lores almost vertical, weakly concave; eye diameter longer than eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, little more than half eye diameter, 0.057–

0.071 of snout-vent; vomerine teeth in long, nearly transverse groups beginning close to anterior margins of choanae, groups separated almost by length of one group.

Tips of fingers dilated into large disks, that of third finger wider than tympanum and about 0.08 of snout-vent; broad web reaching bases of disks of three outer fingers on both edges, to distal border of subarticular tubercle of first finger; a wide flap of skin along outer edge of fourth finger; a supernumerary tubercle on each metacarpal. Tips of toes with disks smaller than those of fingers; all toes broadly webbed to disks; a narrow flap of skin along inner edge of first and outer edge of fifth toe; a small, oval inner, but no outer, metatarsal tubercle; tibia 0.52–0.58 of snout-vent.

Skin finely shagreened above; free of skull; a straight fold from eye above tympanum, ending on shoulder; throat weakly rugose; abdomen coarsely granular; no ridges or flaps of skin on arms, legs, or at vent; a few weak tubercles on lower arm and below vent.

Color (in life) dark reddish brown or clay brown above; dark interorbital bar and dark spots on back present or not; side of head with or without white spots; ventral surfaces white with grayish brown spots: sides and flash surfaces of legs greenish yellow; dark crossbars of limbs usually present, rarely absent; iris hazel green in upper half, dark red in lower. In alcohol, ground color brown or slate above.

Secondary sex characters.—Nine females having mature oviducts measure 60.4–70.4 mm. (mean 66.3); four males having nuptial pads measure 50.0–55.5 mm. (mean 53.4).

The yellowish nuptial pad covers the dorsomedial edge of the first finger from its base to a point just proximal to the level of the subarticular tubercle. At that point the pad expands on the dorsal surface of the finger to form a circular area. It does not extend beyond the level of the subarticular tubercle.

The snout in males projects much more and is longer than that in females.

Ecological notes.—Twenty-three specimens, all for which data are available, were collected in primary rain forest, eight in swamp forest and 15 in hilly forest. All frogs were found on or in vegetation 0.3 to 9 meters above the ground. Two were caught in epiphytes and four in a tree hole. All of the localities are within 300 meters of sea level.

Range.—As specimens are known from both eastern and western Borneo, *harrissoni* must have an extensive range on the island.

SARAWAK: Third Division, Mengiong River; Fourth Division, Baram River, Labang, Sungei Pesu, Ulu Patah River. KALIMANTAN: Long Petah (in Mahakam basin).

Rhacophorus hosei Boulenger. Figure 59.

Rhacophorus hosii Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **16**, p. 169—Patah River, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 253.

Rhacophorus buergeri hosii Wolf, 1936, Bull. Raffles Mus., no. 12, p. 170.

Material examined.—Borneo 64+larvae (1 BM, holotype; 61+larvae FMNH; 1 SM; 1 USNM).

Taxonomic notes.—The inclusion of *hosei* in a "species" consisting of four widely separated groups of forms is another example of the errors resulting from Wolf's extremely broad interpretation of the species. The "species" *buergeri* as Wolf (1936) defined it included long-legged and short-legged forms, smooth-skinned and rough-skinned forms, forms with very little web and forms with almost complete webbing; in short it included such a broad range of character variation as to encompass many valid species.

Rhacophorus macroscelis Boulenger was placed in the synonymy of *hosei* by Wolf; the range of *hosei* surrounds the type locality of *macroscelis*, and the two may occur together on Kina Balu. The morphological differences between them (compare the descriptions given here) are equivalent to those distinguishing known sympatric species of *Rhacophorus*.

A female (USNM 130212) from Kina Balu, previously misidentified as *R. colletti* (Inger, 1954B), is tentatively included here. It differs from the other specimens in having a more depressed and pointed snout and is the only one having a conical tubercle at the heel. If the present identification is correct, *hosei* and *everetti macroscelis* are sympatric.

Description.—Size moderate to small, females 50–65 mm., males 40–50 mm.; body slender; legs long, slender; head obtusely pointed, longer than broad, width 0.34–0.37 of snout-vent, length 0.36–0.41; snout rounded in profile, slightly projecting; nostril twice as far from eye as from tip of snout; canthus sharp, straight; lores slightly concave, sloping very little; eye diameter equal to eye-nostril distance; interorbital narrower than upper eyelid; tympanum distinct, less than half eye diameter, 0.053–0.060 of snout-vent; vomerine teeth in two oblique groups beginning close to anterior borders of choanae, groups widely separated.

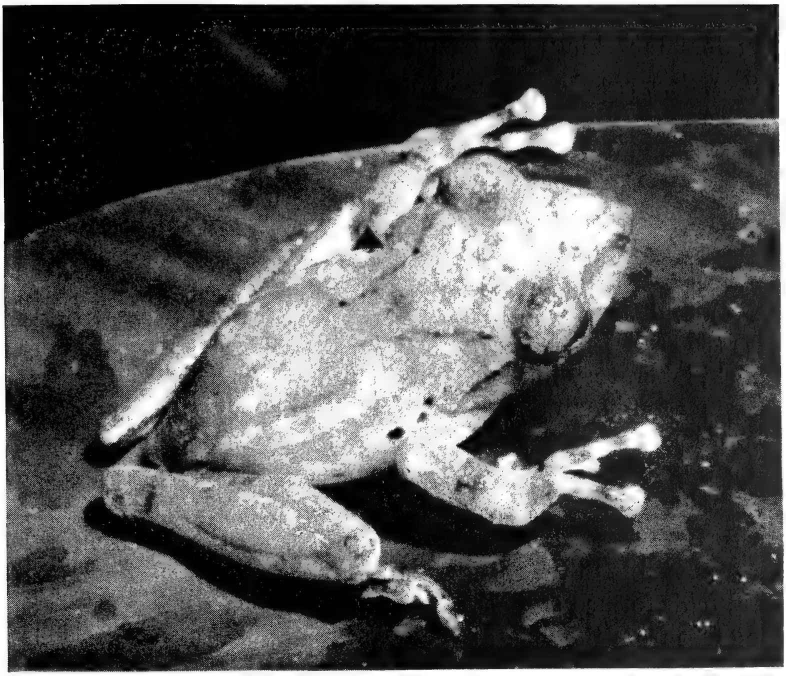


FIG. 59. *Rhacophorus hosei*, adult male, 44 mm.

Tips of fingers dilated into large, round disks, that of third finger equal to or slightly wider than tympanum; web restricted to a narrow fringe at bases of fingers; supernumerary metacarpal tubercles present or not. Tips of toes not as wide as those of outer fingers; first three toes broadly webbed to base of disks on outer edges, fifth toe to base of disk on inner edge; fourth toe broadly webbed to distal subarticular tubercle or just beyond; second toe webbed to tubercle on inner edge, third toe to distal tubercle on inner edge; an oval inner, but no outer metatarsal tubercle.

Skin shagreened above with a few narrow tubercles above shoulders; coarsely granular below, except on throat; a distinctly curved supratympanic fold from eye to axilla; skin free of skull; no dermal appendages on arm or at vent, none along tarsus; one specimen with a small conical tubercle at heel.

Color (in life) yellowish brown to dark sandy brown; interorbital triangle and cruciform pattern of back dark brown; limbs with dark brown crossbars; ventral surfaces white, usually with small brown spots on throat; rear of thighs and tarsi blackish brown or pale sandy

brown; iris greenish gold. In alcohol, dorsal surfaces pale or dark gray; dorsal markings conspicuous only on light ground color.

Secondary sex characters.—Three females containing enlarged ova measure 51.0, 61.3, and 62.0 mm.; 13 males with vocal sacs measure 40.8–49.1 mm. (mean 45.50 ± 0.77). None of these males has nuptial pads or lineae masculinae, yet several were caught in amplexus. The vocal sacs are median, subgular and have round openings near the corners of the mouth. A male 32.5 mm. lacks vocal sacs.

Larvae.—A clutch of eggs was squeezed from a female (FMNH 137874) and artificially fertilized by sperm suspension from two males (FMNH 137871–2) on September 18. The eggs were kept in our field laboratory in a plastic tray containing a few mm. of water. Maximum-minimum temperature range in the forest surrounding the camp clearing during the period of observations on these eggs and larvae was 20.5–31.0° C. The maximum was probably several degrees higher in the camp clearing.

Cleavage was meroblastic. Two days after fertilization a yolk plug was visible in the fertilized and viable eggs. On September 21 neural folds formed and closed. On September 22 the embryos were lifting free from the yolk at the caudal end. By September 27 only seven remained alive. Only one of those had wriggled free of the vitelline membranes.

Fourteen days after fertilization the remaining five larvae died and were preserved. Two of them have fore and hind limb buds. The others appear from their general form and size to have been only a few hours behind this stage. The general body form is oval, the greatest part of the bulk being formed by the yolk mass. The head is very small. The back projects above the yolk mass very slightly. Head-plus-body lengths vary from 5.5 to 6.0 mm. The slender, flexed tails cannot be measured accurately but appear to be slightly longer than the head and body. The eyes are well-formed. The mouth is open but lacks typical tadpole beaks, labial teeth, and expanded lips. Oral suckers are absent. Olfactory pits are visible. There is no sign of external gills, operculum, or coiling of the gut. The length of the hind limb buds is about 1½ times their diameter. The fore limb buds are spheroidal.

The absence of the usual larval oral apparatus and of gills and operculum at early limb bud stages suggests that larvae of *hosei* have an abbreviated free-swimming stage if that stage is not in fact completely suppressed.

Ecological notes.—This species occurs in rain forest, either virgin or partly logged. Twelve were caught at night while calling 30 cm. to 4 m. above ground in shrubs and trees growing on the steep banks of small streams. One juvenile was found under leaves on the forest floor during the day.

The only large series (FMNH 137866–910) was collected at approximately 150 meters above sea level. Other specimens are known from 50 to 600 meters above sea level and to 1375 meters, if the Kina Balu specimen is correctly assigned to this species.

Mature ova are uniformly dark gray with no color differentiation into hemispheres. A clutch of 39 approximately equal-sized eggs was squeezed from one female (FMNH 137874). Only one mature egg (3.8 mm. exclusive of vitelline envelops) remained in the female when she was dissected. Several dozen ova, all less than 1.5 mm. in diameter, were present in each ovary.

The striking difference in color and number between these eggs and those of *Rhacophorus macrotis, otilophus, pardalis,* and *leucomystax,* which are uniformly ivory or yellow and number more than 120 per clutch, suggest a difference in reproductive habits.

Range.—Western and northern Borneo.

SABAH: Ranau District, Bundu Tuhan; Kinabatangan District, Deramakot. SARAWAK: Third Division, headwaters of Baleh River, Mengiong River; Fourth Division, Patah River.

Rhacophorus leucomystax leucomystax Boie

Hyla leucomystax Boie *in* Gravenhorst, 1829, Delic. Mus. Vrat., fasc. 1, p. 26—Java.

Rhacophorus leucomystax Boulenger, 1889, Proc. Zool. Soc. London, **1889**, p. 29; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 246; Smith, 1925, Sarawak Mus. Jour., **3**, p.34; Inger, 1954, Fieldiana, Zool., **33**, p. 376 (part).

Rhacophorus leucomystax leucomystax Wolf, 1936, Bull. Raffles Mus., no. 12, p. 178 (part).

Rhacophorus leucomystax quadrilineatus Inger, *op. cit.*, p. 382.

Material examined.—Borneo 206 (12 BM; 126 FMNH; 24 MCZ; 10 RMNH; 2 SM; 9 SNM; 4 UMMZ; 19 USNM); Mindanao 25 (FMNH); Java 39 (3 AMNH; 3 BM; 1 MCZ; 10 RMNH; 4 SNM; 1 UMMZ; 17 USNM); Sumatra 95 (4 BM; 2 FMNH; 34 MCZ; 1 NHMW; 8 RMNH; 4 UMMZ; 1 USNM; 41 ZMA); Nias 3 (USNM); Malaya 26 (12 FMNH; 14 SNM); Indo-China 17 (16 FMNH; 1 USNM); China 17 (FMNH).

Taxonomic notes.—The Chinese population has been recognized as a distinct subspecies, *leucomystax megacephalus* Hallowell (Pope, 1931), on the basis of the freedom of the skin from the skull. Not only is this distinction confirmed in the Fukien and Szechwan specimens seen, but two others also appear. The head width of the Chinese form (0.330–0.374 of snout-vent in females, 0.343–0.367 in males) is greater than that of the East Indian form (see Table 37). Broad webbing reaches only to the edge of the distal subarticular tubercle or slightly beyond on the third toe in the Chinese frogs, whereas in the typical form it reaches mid-way between the subarticular tubercle and the base of the disk or as far as the disk.

The Philippine populations from Mindanao northward were placed in a separate subspecies, *l. quadrilineatus,* because they were isolated from the typical form of western Borneo, Java, and Sumatra by what was called *leucomystax linki* (Inger, 1954A). But since the latter is shown below (p. 313) to represent a distinct species, *macrotis,* all of the true Philippine *leucomystax* should be placed in the nominate form. As will be seen (*Geographic variation*), the Mindanao population differs from West Bornean, Javan, and Sumatran *leucomystax* only in a few body proportions. These two groups of populations are certainly more similar to one another than either is to the Chinese subspecies, *l. megacephalus* Hallowell.

Description.—Size small to moderately large, males to 50 mm., females to 80 mm.; body slender (males) to moderately robust; limbs long, slender; head longer than broad, obtusely pointed, snout rounded in profile, projecting; nostril much closer to tip of snout than to eye; canthus sharp; lores oblique or vertical, not concave; eye equal to eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, diameter about three-fourths or more of eye diameter; vomerine teeth usually present, in oblique groups between anterior halves of choanae, separated by width of one group, usually closer to choanae.

Tips of fingers dilated into large, round disks having circummarginal grooves; width of largest disk about two-thirds tympanum diameter (Table 37); web between first two fingers not reaching subarticular tubercles, that of outer fingers even less well-developed; a supernumerary tubercle usually on each metacarpal. Tips of toes not as widely dilated as tips of outer fingers; broad web usually reaching bases of disks on outer edges of first three toes and inner edge of fifth toe; fourth toe with two phalanges free of broad web; an oval inner metatarsal tubercle; a small weak, outer metatarsal tubercle present or absent; tibia 0.47–0.60 of snout-vent.

Skin smooth above, with coarse granules below; a narrow dermal fold running horizontally from eye above tympanum to behind arm; a low, narrow, whitish ridge on outer edge of forearm; no other dermal appendages on limbs; skin of head (fig. 60) in all females above

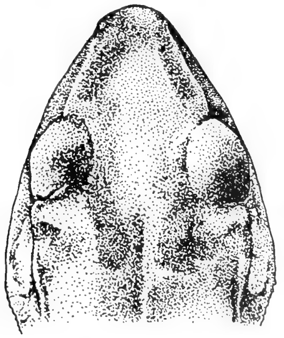


FIG. 60. Dorsal view of head of *Rhacophorus leucomystax*. Dark stippled areas are of skin ossified with skull.

65 mm. involved in ossification of frontoparietals, squamosals, and nasals; in males above 40 mm. skin fused to frontoparietals and, less often, to squamosals.

Color (in alcohol) grayish brown above with four longitudinal dorsal stripes; no interorbital bar; usually a narrow dark stripe just below canthus and another just below supratympanic fold; limbs with dark crossbars; venter whitish, immaculate or with dark spots on throat, rarely dorsum spotted instead of striped.

Secondary sex characters.—Females are much larger than males. The smallest Bornean female containing enlarged ova measures 57.3 mm.; the largest female measures 75.0 mm. The mean of 26 larger than 57.0 is 65.95 ± 0.97 mm. Bornean males having vocal sacs range from 37.3 to 48.2 mm., the mean of 55 being 42.78 ± 0.37 mm. Bornean females have relatively wider heads than do males (Table 37); the difference between the two sets of ratios is statistically significant (Mann-Whitney test: $Z = 3.79$; $P < 0.001$). The sexes do not differ significantly in the other body proportions listed in Table 37.

Males have yellowish nuptial pads covering an oval area on the dorsal and medial surfaces of the first finger from the wrist to the level of the subarticular tubercle, and usually a small circular area on the upper surface of the second finger. The median vocal sac has round bilateral openings near the commissures of the jaws. Lineae masculinae are absent.

TABLE 37.—Comparison of body proportions in samples of *Rhacophorus leucomystax leucomystax.* Proportions given in thousandths of snout-vent.

	Males			Females		
	No.	Range	Median	No.	Range	Median
			Head width			
Mindanao	10	298–318	312		—	
Borneo:						
Kina Balu area	18	298–336	312	11	305–336	316
Beluran	3	298–310	298		—	
Lupar River	14	298–317	307	1	329	
Niah	8	305–324	317	8	315–348	329
combined Bornean	43	298–336	309	20	305–348	321
Java	4	292–348	330	9	317–351	331
Sumatra	10	276–327	317	13	300–342	326
	H*=10.176		P=0.02	H=2.508		P=0.28
			Disk of third finger			
Mindanao	9	50–59	55		—	
Borneo:						
Kina Balu area	9	42–56	49	7	49–55	53
Beluran	3	49–56	52		—	
Lupar River	6	51–56	54	1	58	
Niah	8	47–55	49	8	42–56	51
combined Bornean	26	42–56	51	16	42–58	51
Java	4	41–50	47	9	45–55	50
Sumatra	10	43–57	50	12	47–58	54
	H=12.468		P=0.008	H=5.340		P=0.07
			Tympanum diameter			
Mindanao	10	78–100	90	2	74–82	78
Borneo:						
Kina Balu area	8	66–89	77	5	57–79	73
Lupar River	5	73–80	75	1	73	
Niah	8	77–83	78	8	70–84	79
combined Bornean	21	66–89	78	14	57–84	78
Java	2	79–83	81	4	70–74	73
Sumatra	9	67–85	74	8	67–80	72
	H=18.024		P <0.001	H=3.636		P=0.30

TABLE 37.—Comparison of body proportions in samples of *Rhacophorus leucomystax leucomystax*. Proportions given in thousandths of snout-vent.—(*continued*).

			Tibia length			
Mindanao	10	488–569	515	2	506–508	507
Borneo:						
Kina Balu area	14	472–552	527	6	510–607	514
Beluran	3	500–521	512		—	
Lupar River	10	500–559	533	1	542	
Niah	10	500–564	538	9	519–581	526
combined Bornean	37	472–564	533	16	510–607	526
Java	3	516–551	534	8	495–539	528
Sumatra	10	485–557	536	12	516–586	532
	H=3.732		P=0.29	H=6.120		P=0.11

* H of Kruskal-Wallis analysis of variance; "combined Bornean" sample compared with those of other islands.

Larvae.—No Bornean larvae are available. Tadpoles (fig. 62) from Malaya (Flower, 1896), Sumatra (van Kampen, 1907), and the Philippine Islands (Alcala and Brown, 1956) are similar enough to warrant assuming that Bornean larvae will not differ from them. The larva of *macrotis* resembles that of *leucomystax* so closely that the description of the former (p. 318) may also serve for the latter. The principal differences between the two species are in the labial teeth (I:3–3/III or I:3–3/1–1:II in *leucomystax;* usually I:4–4/1–1:II in *macrotis*) and shape of tail (fig. 62).

Ecological notes.—This species, like *macrotis,* occupies many habitats, but is much more common in towns and cultivation. Of the Bornean specimens for which detailed information is available, 36 were caught in flat, swampy primary forest, 19 in cultivated land, six in old secondary growth, and 15 at an artificial pond.

The ivory-white eggs are laid in foam nests that in the Philippine Islands (Alcala, 1962), China (Liu, 1950), and Java (Zeller, 1960) are attached to vegetation and rocks around the edges of bodies of standing or slowly flowing water. Flower (1896) found *leucomystax* breeding at ponds in Malaya; tadpoles (FMNH 109489) and an egg mass were collected in ponds of the Singapore Botanic Garden by D. Dwight Davis. Presumably the same habits characterize Bornean populations.[1] Clutch size varies from 150 to 900 (Alcala, 1962).

Breeding probably extends over most of the year in Borneo. Almost all males over 37 mm. have nuptial pads, and these specimens

[1] Comments on breeding habits in Borneo (Inger, 1956) properly refer to *Rhacophorus macrotis.*

TABLE 38.—Comparison of samples of *Rhacophorus leucomystax leucomystax*. Sexes combined.

	Outer metatarsal tubercle[1]			Dorsal pattern		
	+/+	+/o	o/o	Striped	Spotted	Uniform
Mindanao	4	3	18	24	1	0
Borneo:						
Kina Balu	15	7	15	40	2	0
Beluran	2	0	1	3	0	0
Lupar River	11	0	4	7	0	0
Niah	10	2	3	56	1	0
Kapuas River	3	0	3	8	1	0
combined	41	9	26	114	4	0
Java	8	1	6	10	9	1
Sumatra	16	2	7	35	25	4
	chi-square=14.931[2]		P=0.02	chi-square=62.5[2]		P <0.001

[1] +/+=present on both feet; +/o=present on one foot only; o/o=absent on both feet.

[2] Calculated using combined Bornean sample; degrees of freedom=6.

were collected in the months of April, July, and August. Approximately two-thirds of females caught in August in northern Sarawak contained enlarged ova.

The altitudinal range in Borneo is extensive, running from near sea level at Kuching and Beluran to 1400 meters on Mount Kina Balu.

Geographic variation.—Local differentiation within Borneo is slight. Of the four body proportions tested (Table 37), the four major Bornean populations differ statistically only in head width (Kruskal-Wallis test: H=8.94; P=0.03). The frequency of specimens lacking an outer metatarsal tubercle is higher in the Kina Balu and Kapuas basin samples than in the others (Table 38) but the differences are not great.

As Tables 37 and 38 show, statistically significant differences exist among populations of *leucomystax leucomystax*. Leg length is the only one of the four body proportions tested that does not show geographic variation in males. The failure of significant differences to appear in females may be a result of smaller sample sizes.

The higher frequency of spotted frogs in the Javan and Sumatran samples is not the result of including populations characterized by all spotted individuals. Each subdivision of these samples includes both types of patterns. For example, a series from Langkat, Sumatra, includes five striped, four spotted, and three uniform frogs.

Another, from Bogor, Java, includes six striped, four spotted, and one uniform. Variability is higher on those two islands than in Borneo or Malaya (10 striped, though three have spots superimposed on the stripes). Two Indochinese samples are like the Malayan and Bornean ones in variability: all seven from near Quang Tri, Annam, are spotted; all five from Phong Saly, Laos, are striped.

Local differentiation of the Chinese populations has been discussed above (*Taxonomic notes*).

Range.—The typical subspecies of *leucomystax* occurs from Hainan (Pope, 1931) and northern Indo-China southward to Java and Borneo and eastward into the Philippine Islands.

SABAH: Jesselton District, Jesselton; Kota Belud District, Kaung, Kiau; Labuk District, Beluran; Penampang District, Penampang; Ranau District, Bundu Tuhan, Tenompok; Tuaran District, Tuaran. SARAWAK: First Division, Kuching, Paku, Sadong, Santubong; Second Division, Engkili; Third Division, Rejang River; Fourth Division, Niah; Fifth Division, Pa Brayong. KALIMANTAN: Nanga Raun, Pagat, Pasir River, Rantau, Rinka, Sangau, Sintang, Smitau.

Rhacophorus macrotis Boulenger

Rhacophorus macrotis Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**, p. 282—Baram district, Sarawak; Taylor, 1920, Phil. Jour. Sci., **16**, p. 285; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 251 (part).

Polypedates linki Taylor, 1922, Phil. Jour. Sci., **21**, p. 276, pl. 3, fig. 2—Jolo Philippine Islands.

Rhacophorus leucomystax linki Wolf, 1936, Bull. Raffles Mus., no. 12, p. 181: Inger, 1954, Fieldiana, Zool., **33**, p. 383; 1956, *ibid.*, **34**, p. 409.

Rhacophorus leucomystax leucomystax (part) Wolf, *op. cit.*, p. 178.

Material examined.—Borneo 141 (1 AMNH; 7 BM, including type of *macrotis*; 1 CAS; 125 FMNH; 3 NSH; 1 SM; 1 USNM; 2 ZMA); Great Natuna 2 (1 BM; 1 CAS); Jolo 3 (MCZ, paratypes of *linki*); Balabac 1 (BM); Palawan 30 (2 FMNH; 28 MCZ); Sumatra 3 (1 BM; 2 RMNH).

Taxonomic notes.—Tree frogs of this form from northeastern Borneo differ from true *leucomystax* in the absence of vocal sacs in males and in the reduction in the amount of dermal ossification on the head (Inger, 1956). These populations, as well as those from Palawan and Jolo in the Philippine Islands, have been referred to *linki* Taylor as a subspecies of *leucomystax* (Wolf, 1936; Inger, 1954A). The holotype and a topotype (AMNH 23762) of *macrotis* agree with specimens

from Palawan, Jolo (paratypes of *linki*), and northeastern Borneo, making it necessary to place *linki* in synonymy.

This form might still be considered a subspecies of *leucomystax* except for two factors: (1) it differs from *leucomystax* in as many ways as do good sympatric species of *Rhacophorus;* and (2) it is sympatric with typical *leucomystax* at widely-separated localities without signs of integradation.

The large series from northeastern Borneo includes 13 specimens, each having two broad, dark, dorsal stripes. The remainder are either spotted (60) or uniform (24) dorsally. True *leucomystax* from the Kina Balu area of western Sabah and from coastal Sarawak usually have four narrow dorsal stripes (89) or two cephalic stripes, each of which branches behind the head forming four stripes on the back (7). The ground color of both forms may be light or dark (in preservative), but the patterns of striping remain distinct. A few *leucomystax* have darkened tympana, but none has the broad, dark temporal band characteristic of *macrotis* (see *Description*).

The body proportions of Bornean *macrotis* and *leucomystax* differ (Table 39). The former has a noticeably wider head and larger digital

TABLE 39.—Comparison of Bornean samples of *Rhacophorus leucomystax* and *R. macrotis*. Body proportions given in thousandths of snout-vent.

	Males			Females		
	No.	Range	Median	No.	Range	Median
			Head width			
leucomystax	43	298–336	309	21	305–348	320
macrotis	44	310–355	336	14	328–364	343
	Z*=7.237		P <0.001	Z=3.922		P <0.001
			Disk of third finger			
leucomystax	26	42–56	51	15	42–56	51
macrotis	32	51–68	60	13	56–70	65
	Z=6.050		P <0.001		Z not calculated	
			Tympanum diameter			
leucomystax	21	66–89	78	14	57–84	78
macrotis	30	81–100	89	13	74–88	81
	Z=5.666		P <0.001	Z=2.547		P=0.01
			Tibia length			
leucomystax	37	472–564	533	16	510–607	526
macrotis	33	487–599	547	16	512–588	544
	Z=3.375		P=0.001	Z=1.715		P=0.08

* Z calculated by means of Mann-Whitney test.

pads. Although *macrotis* also has a longer leg and a larger tympanum, these differences are not as obvious to the naked eye.

In *macrotis* females the lateral edge of the frontoparietal is raised into a low ridge (fig. 61). In a few specimens, e.g., the type of *linki* (Taylor, 1922B, pl. 3, fig. 2) and a female from eastern Borneo (ZMA 5122), the ridge is conspicuously elevated. The edge of the frontoparietal is not raised in *leucomystax*.

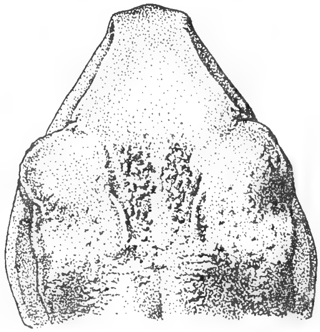


FIG. 61. Dorsal view of head of *Rhacophorus macrotis*.

Larvae of *macrotis* (fig. 62) beyond Stage I have upper labial dental formulae of I:4–4 or, less often, I:5–5 (Inger, 1956; as *leucomystax linki*). Southern Chinese larvae of *leucomystax* (FMNH 24707) in Stage VI have I:3–3, the same count given by Pope (1931) for Hainan tadpoles and the commonest count given by Liu (1950) for western Chinese tadpoles. The same count characterizes *leucomystax* larvae from Malaya (Flower, 1896), Singapore (FMNH 109489), and Sumatra (van Kampen, 1907). Alcala and Brown (1956) state that *leucomystax* larvae from Negros Island in the Philippines have a maximum count of I:3–3 on the upper lip. According to Flower (1899), *leucomystax* tadpoles from Bangkok usually have four interrupted rows of teeth on the upper lip. Larvae of *leucomystax* from China and Malaya have narrower tails than do those of *macrotis* (fig. 62).

Three adult males of *macrotis* and three of *leucomystax* were collected at Beluran, Sabah, by J. A. Tubb. The three *leucomystax* have vocal sacs, four narrow dorsal stripes, and relatively narrow heads (0.298–0.310) and finger disks (0.049–0.056). One of the *macrotis* has two broad dorsal stripes and the others are spotted; all three have wide heads (0.331–0.332) and disks (0.059–0.064) but no vocal sacs. All six Beluran males have nuptial pads. Six adults (2 females, 4 males) of *leucomystax* and two adult males of *macrotis* were

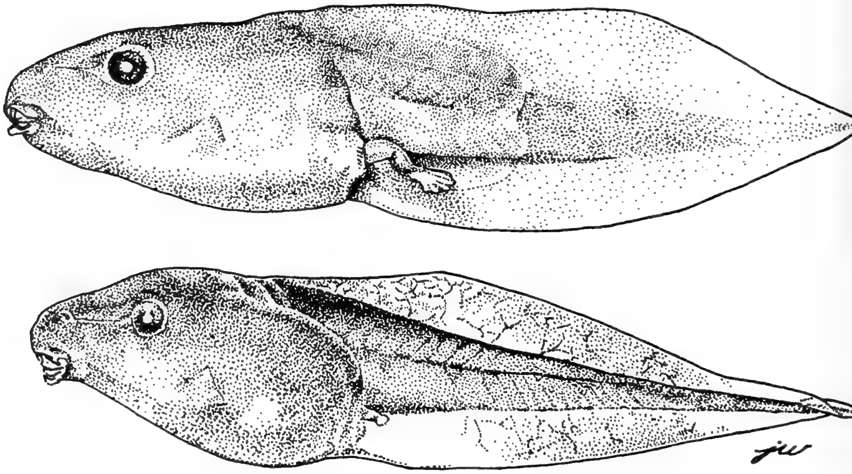


FIG. 62. Tadpoles of *Rhacophorus macrotis* (upper) from Sabah and of *Rhacophorus leucomystax* (lower) from Singapore.

collected at Ranau, Sabah by Dr. Robert Kuntz. All of the *leucomystax* have four narrow stripes; the males have vocal sacs. One *macrotis* has two broad stripes and the other small dark spots; both have nuptial pads but no vocal sacs. Two *macrotis* having the characteristic black temporal stripe and wide finger discs and more than 50 *leucomystax* lacking the temporal stripe and having narrow finger discs were collected at Niah, northern Sarawak.

A series of eight frogs (collection of Rijksmuseum van Natuurlijke Historie) from Fort de Kock, western Sumatra, includes two adult females of *macrotis* and six *leucomystax*, two of which are adult males and three subadult females. The large females have the broad heads (0.334–0.372), wide finger discs (0.070–0.073), and reduced dermal ossification of *macrotis* (c.f. Table 39). The adult males have vocal sacs, narrow heads (0.309–0.327), and narrow disks (0.043–0.052) as in *leucomystax* (Table 39). The subadult females also have narrow heads (0.304–0.315) and disks (0.047–0.055). Four of the six *leucomystax* each have four narrow dorsal stripes; the other two are faded. The two *macrotis* are spotted dorsally. Thus the two forms occur together without intergradation.

Description.—Size small to moderately large, males to 60 mm., females to 90 mm.; body robust (female) to moderately slender (male); limbs long, slender; head broad, triangular, obtusely pointed; snout rounded in profile, projecting; nostril much closer to tip of snout

than to eye; canthus sharp; lores concave, oblique; eye equals eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, diameter about three-fourths eye diameter; vomerine teeth in transverse or oblique groups between anterior halves of choanae, groups usually closer to choanae than to each other.

Tips of fingers dilated into large disks having circummarginal grooves, disks two-thirds to three-fourths tympanum diameter (Table 39); web between first two fingers rarely reaching bases of subarticular tubercles; web between other fingers even less well-developed; a small supernumerary tubercle on each metacarpal. Tips of toes not as widely dilated as those of outer fingers; broad web usually reaching bases of disks on outer sides of first three toes and on inner side of fifth; fourth toe with two phalanges free of broad web; a round or oval inner metatarsal tubercle; outer metatarsal tubercle absent or present as small, round structure; tibia 0.49–0.60 of snout-vent (Table 39).

Skin above smooth or with minute spinose tubercles; ventrally coarsely granular; a conspicuous, narrow dermal fold extending horizontally from eye above tympanum to behind arm; a low, whitish dermal ridge along outer edge of forearm; no flaps of skin along arm or leg; no dermal appendage at heel; two or four low, but conspicuous white tubercles below vent; skin of the head involved in ossification of frontoparietals in all adult females and in most males larger than 50 mm.; skin of head otherwise free of ossification.

Color (in alcohol) grayish brown above; dorsum uniform, spotted, or with two broad, dark stripes beginning on snout; about half of uniform or spotted individuals have a narrow interorbital bar; a broad, dark lateral stripe beginning behind the eye, covering the entire tympanum, and extending for shorter or longer distance behind arm; limbs with dark crossbars above; venter whitish, with or without small dark spots.

In life dorsal ground color varied from cinnamon brown to pale yellowish brown.

Secondary sex characters.—Adult females are much larger than males, 15 females from Borneo measuring 67.5–84.6 mm. (mean 74.14 ± 1.24) and 45 males with nuptial pads 44.9–57.4 mm. (mean 51.18 ± 0.39). Females have relatively wider heads and finger tips and relatively narrower tympana. The difference between the sexes in these ratios (see Table 39) are statistically significant, the values of P (derived from the Mann-Whitney test) being, respectively, <0.001, <0.001, and 0.01.

The yellowish nuptial pads cover the dorsal and medial surfaces of the first finger from its base to the level of the subarticular tubercle and a small oval area on the dorsal surface of the second metacarpal. Pinkish lineae masculinae are present at the dorsal and ventral borders of the obliquus muscle in males. Vocal sacs are absent.

Larvae.—Identification is based on a developmental series complete through metamorphic stages (Inger, 1956). The following description is based on a Stage IX larva (FMNH 63550) from northeastern Borneo (fig. 62, upper).

Body oval in plan view, flat above, rounded below; eyes dorsolateral, visible from below, at end of anterior third of body; internarial distance equal to eye-nostril distance, much less than interorbital.

Oral disk ventral, subterminal, less than half width of body; a staggered row of short papillae bordering lower lip, a very narrow median interruption; papillae continued on to lateral quarters of upper lip; labial teeth I:4–4/1–1:II, the interruption in the innermost lower row narrow; all lower tooth rows extending width of oral disk; beaks strong, finely serrated, entirely black; upper beak with slight median convexity (fig. 63).

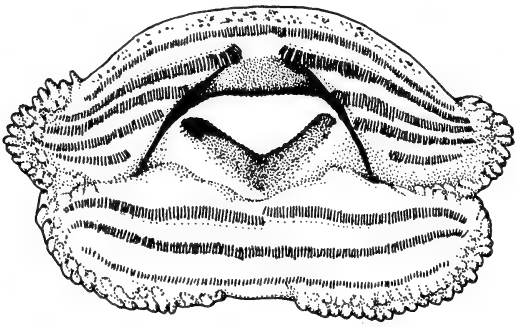


FIG. 63. Oral disk of tadpole of *Rhacophorus macrotis* from Sabah.

Spiracle sinistral, not tubular, opening in center of body below line from eye to root of limb bud; anus dextral, opening at mid-depth of ventral fin.

Tail weak, convex, deeper than body at center, abruptly tapered in last quarter to slender, drawn-out tip; dorsal fin rising from end of body to center of tail, deeper than ventral fin and several times deeper than caudal muscle at center.

Color (in life) dorsally speckled with green, black, and yellow, giving general appearance of dark green with scattered light flecks; ventral surface silvery gray; base of caudal muscle with reticulation of dark pigment; proximal third of fins opaque from muscle half way to fin margins; opaque area of upper fin dark as body, that of lower fin white with small dark dots; remainder of fins transparent with scattered melanophores.

Younger larvae tend to have more spheroidal bodies, though the dorsal surface is usually flattened. Otherwise the body form agrees with the above description. Labial tooth counts of larvae from Sarawak and Sabah in stages of hind limb development vary from I:4–4 (16 specimens) to I:5–5 (1) on the upper lip and 1–1:II (15) to III (2) on the lower. In pre-metamorphic stages a narrow interorbital bar appears and three to five dark crossbars develop on the hind limbs. At the same time the dorsal fin acquires dark blotches.

Ecological notes.—*Rhacophorus macrotis* is abundant in the edges of secondary growth and primary rain forest and in large clearings surrounded by tall secondary growth or forest. Of 86 mature frogs I collected, one was in primary rain forest, two in logged forest, 49 at the edge of logged forest, 31 in large clearings surrounded by logged forest, and three in houses. Most of these specimens were males calling from the ground or in vegetation (up to three meters high) around small pools of standing water. In such situations it is often found with *Rhacophorus otilophus* and *R. pardalis* and less often with *R. appendiculatus*.

The foam nests are attached to shrubs or small trees overhanging small pools or to grass or herbs at the edge of pools. All the larvae I collected were caught in stagnant water. In some cases the pools were in the center of clearings 50 meters wide and not overhung by any trees. Most of the pools were at the edges of clearings and were at least partially covered by trees or shrubs.

All of the eastern Sabah localities from which *macrotis* is known are within 200 meters of sea level. Twenty-one frogs were collected in the Kelabit highlands between 1000 and 1200 meters above sea level.

Calling aggregations were observed May to August in two years. Most (9/14) of the females collected during the same period contained mature ova. Several pairs were caught in amplexus. Males collected in the Kelabit highlands in November had fully developed nuptial pads. *Rhacophorus macrotis* males have a strong call despite the absence of vocal sacs.

Geographic variation.—Within Borneo geographic variation is minor and, for the characters studied, is found only in the relative width of the disk of the third finger. In the following tabulation, the range of the ratio of disk width to snout-vent (given in thousandths) in males of each population is followed in parentheses by the median and number of specimens: Sapagaya 56–68 (61; N=8); Beluran 59–64 (60; N=3); Bukit Kretam 54–61 (58; N=10); Kalabakan 56–66 (60; N=10). All of these localities are in eastern Sabah. The differences between the populations were tested by the Kruskal-Wallis analysis of variance (Siegel, 1956) and were statistically significant (P=0.045). The other body proportions listed in Table 39 show no geographic variation in Borneo.

As already noted (Inger, 1954A), Palawan males are smaller than those from Borneo, the means for the two populations being 43.55 ± 0.39 and 51.18 ± 0.39 mm., respectively. Palawan males also have narrower heads (0.297–0.344; median=0.314) than Bornean males (0.310–0.355; median=0.336); the difference between the two distributions is significant at the P=0.001 level (Mann-Whitney U test).

Range.—Sumatra, Natuna Islands, Borneo, Palawan, and the Sulu Archipelago.

SABAH: Kinabatangan District, Deramakot; Labuk District, Beluran; Lahad Datu District, Lahad Datu, Silabukan valley; Ranau District, Ranau; Sandakan District, Sandakan, Sapagaya Forest Reserve; Tawau District, Kalabakan, Sebatik Island. SARAWAK: First Division, Tandjong Datu; Third Division, Mengiong River; Fourth Division, Bario, Long Lelang and Long Siniai on the Akah River, Niah, Pa Main near Bario. KALIMANTAN: Balikpapan, Semberrah, Sungei Batu Lepo (near Sangkulirang).

Rhacophorus nigropalmatus Boulenger

Rhacophorus nigropalmatus Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **16**, p. 170—Akah River, Sarawak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 266; Smith, 1925, Sarawak Mus. Jour., **3**, p. 34.

Rhacophorus nigropalmatus nigropalmatus Wolf, 1936, Bull. Raffles Mus., no. 12, p. 200.

Rhacophorus rheinwardti (nec Boie) Peters, 1872, Ann. Mus. Civ. Genova, **3**, p. 45.

Material examined.—Borneo 12 (3 BM; 5 FMNH; 1 MCG; 1 SM; 2 ZMA); Sumatra 4 (2 NMB; 1 RMNH; 1 ZMA); Malaya 1 (BM).

Taxonomic notes.—The specimen listed above from the Museo Civico of Genoa (MCG) is the one incorrectly identified as *reinwardti* by Peters (1872).

Wolf (1936) made every large green *Rhacophorus* having moderately extensive webbing a subspecies of *nigropalmatus*, apparently without regard to the great differences distinguishing these forms. One of them, *georgii* Roux of Celebes (type examined), differs from all of the others in having the skin co-ossified with the skull and from all other species in the genus in having four bony occipital knobs. It further differs from *nigropalmatus* in having smaller feet, the first two fingers webbed only at the base, and no broad flaps of skin on forearm and tarsus.

Rhacophorus feae Boulenger of Burma (type examined) also lacks the broad dermal appendages of *nigropalmatus*; has less extensively webbed fingers, smaller feet (0.44 of snout-vent, 0.50–0.59 in *nigropalmatus*), and shorter legs (tibia 0.48 of snout-vent, 0.54–0.58 in *nigropalmatus*); and lacks black pigment on the web.

Rhacophorus dennysi Blanford of southern China (8 examined) lacks the dermal appendages of *nigropalmatus* and has much less webbing on the hand, smaller feet (0.42–0.46), shorter legs (tibia 0.45–0.48), a differently shaped head, and no black pigment on the web. According to Wolf's notes (1936, p. 203), *R. maximus* Günther of northern India differs from *nigropalmatus* in the same characters as does *dennysi*.

The four species (*georgii, feae, dennysi,* and *maximus*) Wolf treated as subspecies of *nigropalmatus* are no more similar to it than is *reinwardti*, which Wolf considers to be a distinct species. In Sumatra *nigropalmatus* and *reinwardti* are sympatric without loss of their distinctiveness. As the four questionable forms differ from *nigropalmatus* as much and in the same characters as *reinwardti*, it is wiser to refer to them as full species.

Description.—Size large, males to 90, females to more than 100 mm.; body moderately slender to stocky; limbs long, slender; head as broad as long or slightly broader; head width 0.33–0.36, length 0.32–0.37 in snout-vent; snout round when viewed from above, truncate or sloping forward a little in profile, not projecting; nostril near end of snout; canthus distinct; lores sloping, weakly concave; eye diameter greater than eye-nostril distance; interorbital much wider than upper eyelid; tympanum distinct, one-half to two-thirds eye diameter; vomerine teeth in transverse groups beginning at anterior edges of choanae, groups usually separated by less than length of one group.

Tips of fingers dilated into large, transversely oval disks, that of third finger much wider than tympanum; all fingers fully webbed to

disks; inner edge of first finger and outer edge of fourth with broad flaps of skin; supernumerary metacarpal tubercles usually present. Tips of toes dilated but disks not as wide as those of outer fingers; full web reaching disks of all toes; web not excised; inner edge of first toe and outer edge of fifth with broad flaps of skin; an oval inner but no outer metatarsal tubercle; foot, measured from base of inner metatarsal tubercle to tip of fourth toe, 0.50–0.59 of snout-vent; tibia 0.54–0.58.

Skin shagreened above; coarsely granular below, except smooth on throat; no supratympanic fold; a broad (about two-thirds diameter of tympanum) flap of skin on outer edge of forearm; a broad, smooth-edged flap of skin at tibio-tarsal joint, continued as a slightly narrower flap along edge of tarsus.

Color (in life) green above, with or without circular white spots on dorsal surface of thighs; varying from yellowish green to dark leaf green depending on exposure to light, animal darkest after long exposure; sides of body, anterior and posterior edges of upper arm and hind limb, and anterior edge of forearm bright orange-yellow; medio-dorsal surface of tarsus, dorsal surface of two inner fingers and three inner toes greenish yellow; web of hands and feet heavily marked with black from bases of digits to edge of membrane; ventral surface of head and body white; iris pale gold.

In alcohol the dorsal surfaces are violet or slate gray, the sides and ventral surfaces cream-colored.

Secondary sex characters.—Females are larger than males. The snout-vent range of six males having nuptial pads is 78.7–88.6 mm. (mean 84.1), of five females with enlarged ova 89.0–100.3 mm. (mean 95.0). The sexes do not differ in body proportions.

Males lack vocal sacs but have yellowish nuptial pads on the first fingers. The pad covers a small oval area on the dorsal surface of the first finger above the subarticular tubercle. A thin pinkish linea masculina runs along the dorsal border of the obliquus muscle.

Larvae.—Several series of tadpoles (FMNH 77544, 77548, 137912–20) ranging from pre-limb bud to advanced metamorphic stages are tentatively assigned to *R. nigropalmatus*. They have sinistral spiracles, the vent dextral and not reaching the margin of the ventral fin, and papillae of the upper lip confined to the corners; these larval characters plus the large digital disks and extensive webbing of the fingers in advanced larvae confirm the generic identification.

The two most advanced (Stages XIX and XXII) have the three outer fingers webbed to the disks. The web between the first and

second fingers reaches the center of the subarticular tubercles. They also have narrow, smooth-edged fringes of skin along the lower arm, along the tarsus, and at the heel. Only four species of Bornean *Rhacophorus* have this type of dermal appendage at these points: *dulitensis, pardalis, baluensis,* and *nigropalmatus.*

Larvae of *R. dulitensis* in metamorphic stages have the transverse supra-anal flap typical of that species (pp. 296-297); they differ in coloration and labial dentition from the present series. Larvae assigned to *pardalis* (p. 331) differ in the same characters. The identification of so-called *pardalis* tadpoles may be questioned. However, the ratio of hand length to snout-vent of metamorphosing *pardalis* larvae (0.32) agrees with that of adult *pardalis* (0.30–0.31), whereas the ratio in the present advanced larva (0.38) matches that in adult *nigropalmatus* (0.37–0.38).

Rhacophorus baluensis has been collected only at high elevations, *nigropalmatus* only at low elevations. These larvae were collected within 300 meters of sea level. The hand ratio of the transforming tadpole is more similar to that of adult *nigropalmatus* than to that of single adult *baluensis* (0.33) available. For these reasons, it is more likely that the present larvae belong to *nigropalmatus* than to *baluensis.*

The larvae differ from adult *nigropalmatus* in having less webbing between the first two fingers. The webbing may become more extensive later in development, but this difference leaves the identification tentative.

The following description is a composite based on 18 larvae.

Body ovate, flattened above and below; eyes dorsal, not visible from below; diameter of eye subequal to eye-nostril and internarial distances, about two-thirds of interorbital distance; spiracle sinistral, non-tubular, below line connecting eye and root of hind limb, about midway between eye and root of hind limb; anus dextral, opening not reaching margin of ventral fin.

Mouth ventral, subterminal; beaks black-edged, finely serrate, upper one a smooth arc; papillae small, homogeneous, in a double row narrowly interrupted or continuous across lower lip, confined to lateral corners of upper lip; teeth on upper lip I:3–3 (1 specimen), I:4–4 (12), I:4–5 (1), I:5–5 (1), II:4–4 (1); teeth on lower lip 1–1:II (16); gaps in divided inner row of lower lip and of outermost divided row on upper lip very narrow.

Tail 0.58–0.65 of total length, heavy, moderately convex, tapering to a point; dorsal fin beginning at end of body; caudal muscle deeper than either fin in proximal three-fifths or two-thirds.

Color (in life) of head and body pale gray above, lighter below, no markings; tail pale gray with conspicuous black spots on fins and caudal muscle; a thin dark line on edge of dorsal fin and usually on edge of ventral one.

While kept in the laboratory, the tadpoles became paler, though the black spots remained visible.

Sizes (mm.) at various stages are:

STAGE	NO.	HEAD-PLUS-BODY	TOTAL
pre-limb bud	4	6.8–11.2	16–28
I	1	9.3	..
II	1	13.6	36
IV	2	12.4–14.6	..
XI	1	14.7	39
XII	1	14.7	43
XIV	3	16.9–17.9	47–50
XV	1	17.0	48
XVI	2	16.4–18.2	44–50
XVII	1	17.5	43
XVIII	1	17.0	48
XIX	1	17.4	47
XXII	1	16.6	17.6

The stage XIX larva has lost the beaks and labial teeth; papillae are still present at the corners of the mouth. The gape of the stage XXII larva has reached a perpendicular from the center of the eye; the tympanum is not visible.

Larvae from Sabah (FMNH 77544, 77548) have smaller eyes than those from Sarawak. The diameter of the eye is about one-third the internarial distance in the tadpoles from Sabah, whereas in those from Sarawak the eye is almost equal to the internarial width.

Ecological notes.—*Rhacophorus nigropalmatus* has been collected in Borneo only at elevations within 300 meters of sea level. The five specimens for which data are available were caught in primary rain forest (3) and logged rain forest (2). One was caught on the ground and four on low vegetation between one and two meters above ground.

One frog was thrown into the air from a height of five meters above ground. It immediately righted itself and held the hands and feet in the plane of the body with the digits widely spread. Two others were forced to jump from approximately the same height and assumed the same posture in the air. *Rhacophorus pardalis* and *otilo-*

TABLE 40.—Lengths of forced leaps of three species of *Rhacophorus*. Height of launching site 5.4 meters.

Species	Snout-vent	Area of foot (mm.²)	Trial no.	Time (sec.) to ground[1]	Horizontal length of leap (m.)[2]
otilophus					
77048	85.6	265	1	1.0	4.0
			2	1.0	3.0
77044	71.6	194	1	1.0	3.67
pardalis					
77005	43.1	188	1	1.4	3.2
			2	1.3	3.2
77006	41.9	188	1	1.2	2.5
nigropalmatus					
76998	88.6	1107	1	1.2	4.8
			2	1.4	5.0
			3	1.6	7.3

[1] Slight inaccuracies may enter into this measurement because of the reaction time of the observer. However, assuming the same reaction time on each trial, these measurements at least indicate an order among trials.

[2] Measured from plumb point below launching site to landing point on ground.

phus also spread the digits when obliged to jump from heights. When thrown into the air *otilophus* turns over two or three times before orienting parallel to the horizon. *Rhacophorus pardalis* holds the hands and feet above the plane of the body (Inger, 1956).

These three species were stimulated to jump from a height of 5.4 meters by pinching the ends of their bodies. Although the height is probably not great enough to allow gliding ability to operate fully, if at all, the differences among the species (Table 40) in time to the ground reflect the differences in amount of webbing. The absolute area of the foot of *otilophus* is greater than that of *pardalis*, but the area relative to the body mass is much greater in *pardalis*. The area of the foot is both relatively and absolutely larger in *nigropalmatus* than in *otilophus*. The hand of *otilophus* is without web, placing the species still farther behind the other two in amount of braking or parachuting surfaces. The differences in horizontal length of jump are more difficult to interpret. Possibly the greater absolute size of the leg of *nigropalmatus* accounts for its longer leap.

The gliding leap ascribed to *nigropalmatus* by Boulenger (1912, after Wallace) was not observed. Sufficient height in a cleared area was not available.

Geographic variation.—The few Sumatran and Malayan specimens do not differ from those of Borneo in the characters studied.

Range.—Malay Peninsula, Sumatra, Borneo, and Thailand (Taylor, 1962). Smith (1930) referred to a single specimen from northern Thailand; before this locality is included in the range of *nigropalmatus* the specimen should be compared to *Rhacophorus feae.*

SABAH: Kinabatangan District, Deramakot; Tawau District, Kalabakan. SARAWAK: First Division, Bidi, Kuching; Third Division, Nanga Tekalit; Fourth Division, upper Baram, Akah River (Boulenger, 1895). KALIMANTAN: Buntok, Semberrah River.

Rhacophorus otilophus Boulenger. Figure 64.

Rhacophorus otilophus Boulenger, 1893, Proc. Zool. Soc. London, **1893**, p. 527, pl. 44—Bongon, Sabah; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 245; Smith, 1925, Sarawak Mus. Jour., **3**, p. 34; Wolf, 1936, Bull. Raffles Mus., no. 12, p. 184; Inger, 1956, Fieldiana, Zool., **34**, p. 413, figs. 89–90.

Material examined.—Borneo 46+larval series (6 BM; 31+larvae FMNH; 2+larvae RMNH; 5 SM; 1 UMMZ; 1 USNM).

Description.—Size moderate to large, males to 80 mm., females to 95 mm.; body robust; limbs slender, short; head triangular, longer than broad, head width 0.34–0.39 of snout-vent; a sharp triangular bony process at commissure of jaws, a serrated bony crest projecting above tympanum; snout rounded in profile, projecting; eye-nostril distance more than twice that between nostril and snout; eye subequal to eye-nostril distance; interorbital wider than eyelid; tympanum conspicuous, oval, horizontal diameter two-thirds to three-fourths eye, 0.07–0.08 of snout-vent; vomerine teeth in oblique groups between anterior halves of choanae, groups closer to choanae than to each other.

Tips of fingers expanded into large disks, that of outer fingers only slightly narrower than tympanum diameter; a rudiment of web between first two fingers, none between outer ones; metacarpals with supernumerary tubercles. Tips of toes expanded into disks much smaller than those of outer fingers; broad web to subarticular tubercle of first toe, to between tubercle and base of disk on outer edge of second and third and on inner edge of fifth, to middle tubercle of fourth toe; web sometimes less extensive; an oval inner metatarsal tubercle; no outer one; tibia 0.47–0.55 of snout-vent.

Skin above smooth or with whitish spinose asperities; sides and abdomen with coarse granules; a small, triangular dermal appendage at heel and, often, at elbow; a row of four to six enlarged, white tubercles below vent; a white dermal fringe sometimes present above

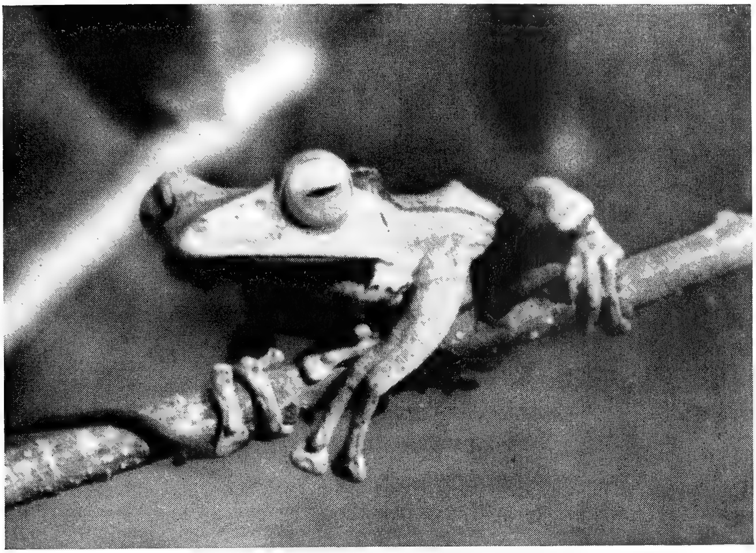


FIG. 64. *Rhacophorus otilophus*, 79 mm.

vent; skin of head co-ossified with roof of skull, except, rarely, in prefrontal region.

Color (in life) lemon yellow above with numerous thin black, longitudinal lines; thighs with seven to ten, narrow black bars on anterior and posterior faces; below cream-colored or white. In alcohol dorsal color fades to gray or brown.

Secondary sex characters.—Females available (11) have snout-vent lengths of 82.4–96.5 mm. (mean 89.15 ± 1.49); the smallest contained enlarged ova. Males with vocal sacs range from 63.8 to 80.5 mm. (mean 72.72 ± 0.79; $N = 29$). The sexes do not differ in relative head width, tympanum diameter, or tibia length.

Males have median subgular vocal sacs with round, bilateral openings near the jaw commissures. The nuptial pads are grayish or yellowish velvety structures covering the dorsal and medial surfaces of the first finger from the wrist to the level of the subarticular tubercle and a circular area on the dorsal surface of the second finger. Pink lineae masculinae are present at dorsal and ventral borders of the obliquus muscle.

Larvae.—Tadpoles (fig. 65) at all stages of development agree with Boulenger's description (1893A); the metamorphic and premetamorphic stages have the diagnostic coloration of adults.

Body spheroidal, top of head flattened; eyes dorsolateral, visible from below; nostril much closer to tip of snout than to eye; eye-nostril distance equals internarial.

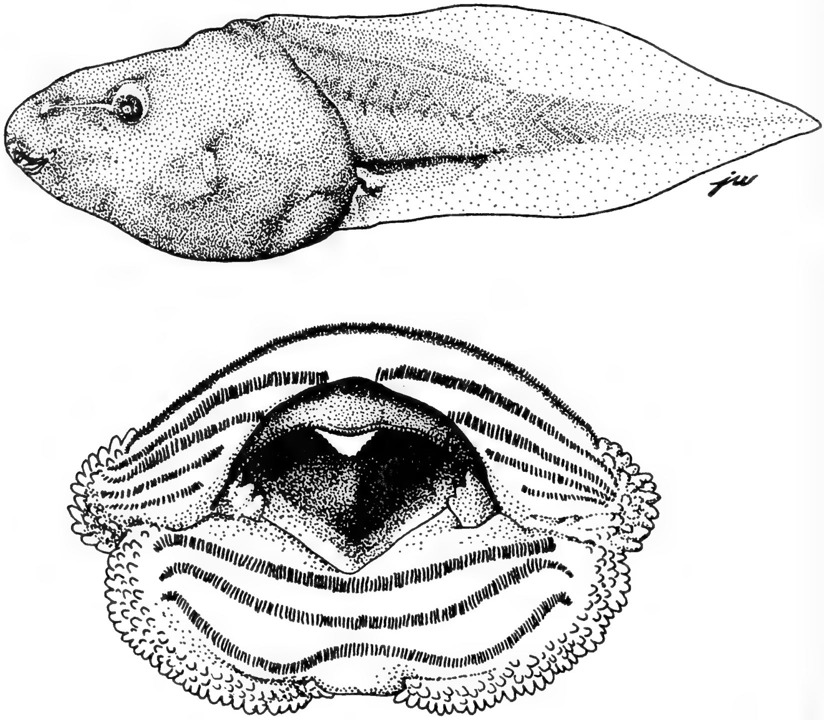


Fig. 65. Tadpole of *Rhacophorus otilophus* from Sabah.

Oral disk ventral, subterminal, about one-third body width; papillae in double, staggered row along margin of lower lip and at corners of upper lip, a gap in papillae at center of lower lip; labial teeth usually I:3–3/III, rarely I:4–4/III, in larvae in hind limb stages; beaks strong, black, denticulated, upper one with pronounced convexity at center.

Spiracle sinistral, non-tubular, below line between eye and insertion of hind limb, closer to eye than to tail; anus dextral, not reaching margin of ventral fin.

Tail convex, deepest at center, tapering to long narrow tip; caudal muscle weak; both fins deeper than muscle beyond basal third of tail.

Color (in life) yellowish green above, white below. Larvae acquire adult pattern on body and hind limbs before eruption of fore limbs.

Larvae in Stage I have total lengths of 26–31 mm. of which the tail forms 0.54 to 0.58. Total lengths in premetamorphic stages reach 53–57 mm.

At hatching, larvae have fully developed eyes, external gills, open mouth, and oral suckers; labial teeth, papillae, and beaks are absent. By the third day after hatching, the operculum has closed and oral suckers are still present. On the fourth day, the first coil of the gut appears. Beaks and labial papillae are present on the fifth day. Details of subsequent development are given elsewhere (Inger, 1956).

Ecological notes.—*Rhacophorus otilophus* lives in secondary growth, at the edges of primary forest, and even in villages. None of the 29 for which detailed information is available was caught in primary forest. A logged area, in which the few remaining tall trees were separated by a dense tangle of young secondary growth, formed a typical habitat at Kalabakan, Sabah. At night in such places, *otilophus* calls from low vegetation (usually less than two meters from the ground) around small temporary pools. Several foamy masses of eggs were found attached to low herbs (*ca.* 30 cm. above ground) around one pool and a pair in amplexus was caught at the same height and place.

Two specimens were collected at 400 meters above sea level in the upper Akah River drainage. Six others are from 200 meters and 30 from less than 100 meters above sea level.

Males with nuptial pads were calling in the months of April, May, and June. Ovulated females, foam nests, and larvae of various stages were collected during the same period. The full extent of the breeding season is not known.

Geographic variation.—Frogs from Sarawak and Kalimantan do not differ from the Sabah samples in the characters examined.

Range.—Borneo and Sumatra (van Kampen, 1905). The single Sumatran specimen known was collected near Palembang in southeastern Sumatra. Van Kampen's notes leave no doubt as to the identification.

SABAH: Kinabatangan District, Bukit Kretam; Kudat District, Bongon (Boulenger, 1893A); Labuk District, Beluran; Sandakan District, Bettotan, Sandakan; Tawau District, Kalabakan. SARAWAK: First Division, Buso, Matang; Third Division, Rejang District; Fourth Division, Long Akah, Long Datih (upper Akah River), Niah, Long Siniai. KALIMANTAN: Long Bluu (upper Mahakam).

Rhacophorus pardalis pardalis Günther

Rhacophorus pardalis Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 83, pl. 6, fig. D—Philippines and Borneo; Boulenger, 1882, *ibid.*, ed. 2, p. 91; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 263; Smith, 1931, Bull. Raffles Mus., no. 5, p. 18.

Rhacophorus pardalis pardalis Wolf, 1936, Bull. Raffles Mus., no. 12, p. 204; Inger, 1954, Fieldiana, Zool., **33**, p. 370, fig. 66; 1956, *ibid.*, **34**, p. 417, fig. 91.

Rhacophorus pulchellus Werner, 1900, Zool. Jahrb., **13**, p. 495, pl. 33, fig. 7—Djapura, Sumatra.

Rhacophorus pardalis pulchellus Wolf, 1936, *op. cit.*, p. 207.

Material examined.—Borneo 94 (8 BM; 70+larvae FMNH; 3 MHNP; 6 RMNH; 4 SM; 3 ZMA); Sumatra 1 (NMB, type of *pulchellus*); Mindanao 12 (3 FMNH; 9 UMMZ); Basilan 4 (CAS); Luzon 2 (CAS); Negros 1 (FMNH).

Taxonomic notes.—Examination of the type of *pulchellus* and larger series from Borneo confirms my previous opinion (Inger, 1954A) that *pulchellus* is a strict synonym of *pardalis.* Differences between the Bornean and Philippine samples exist (see below, *Geographic variation*), but differentiation has not reached a level warranting subspecific recognition. Wolf's (1936) statement that the white spots found in Philippine specimens did not appear in those from Borneo was based on an inadequate sample; white spots are common in Bornean *pardalis.*

Description.—Size small to moderate, males to 55 mm., females 60–75 mm.; body slender to moderately robust; limbs long, slender; head longer than broad; snout obtusely pointed or rounded, projecting slightly; nostril much closer to tip of snout than to eye; canthus distinct; lores sloping, weakly concave; eye diameter equals eye-nostril distance; interorbital usually wider than upper eyelid; tympanum distinct, about half eye diameter; vomerine teeth in oblique or transverse groups beginning at anteromedial corners of choanae, groups widely separated.

Tips of fingers dilated into large disks, those of outer fingers subequal to diameter of tympanum; web between first two fingers reaching distal edge of subarticular tubercles of first and second fingers or beyond; web between second and third and between third and fourth fingers reaching disks of all fingers; fourth finger with one subarticular tubercle; supernumerary metacarpal tubercles usually present. Tips of toes with large disks, though smaller than those of outer finger; broad web reaching disks of all toes; a small, oval, inner metatarsal tubercle; no outer one; tibia 0.47–0.59 of snout-vent.

Skin finely shagreened above, coarsely granular below except smooth on throat of female; skin of head free from skull; broad, smooth-edged flaps of skin along forearm and tarsus extending along outer edges of fourth finger and fifth toe; a broad, round flap at heel; no dermal appendages at vent.

Coloration in life highly variable; ground color usually light tan with or without dark interorbital bar, dark cruciform pattern on back, or dark, dorsal spots; dorsum usually spotted irregularly with brown, black, blue, yellow, and orange; sides spotted with black; abdomen in many specimens with a deep orange network on pale lemon yellow; webs of hands and feet orange red. In alcohol dorsum usually light tan with or without darker markings; limbs with dark crossbars.

Secondary sex characters.—Females are about 15 mm. larger than males. Three gravid females from Kalabakan measure 54.0–57.0 mm., as compared to 38.7–46.5 mm. for males. Four females from Sarawak measure 64.2–71.6 mm., males from the same area 49.6–55.4 mm.

Contrary to previous statements (Liu, 1935; Inger, 1954A), the subgular vocal sac is paired in *pardalis* (males from the Philippines and Borneo dissected). The two sacs are narrowly separated near the mid-line and careless dissections may explain previous misstatements. The round openings are near the jaw commissures.

Weak nuptial pads consisting of clusters of glandules not differing in color from the adjacent skin occupy the dorsomedial surface of the first finger. Pinkish lineae masculinae are present at dorsal and ventral borders of the obliquus muscle in mature males.

Larvae.—Sabah tadpoles hatching from a typical rhacophorid froth nest brought into the laboratory agree in color pattern, dentition, and labial papillae with larvae having the forelimbs well enough developed for comparison with adults (Inger, 1956). Several species of Sarawak larvae agree in dentition, labial papillae, and form of beaks and tail with the ones from Sabah, but differ in intensity of coloration, and in degree of development of the lateral line system. The hand of a Stage XIV Sarawak larva agrees with the adult *pardalis* from the same area and has only slightly more webbing than a tadpole from Sabah; this difference between the larvae parallels a difference between adults (see *Geographic variation*).

Body spheroidal, flattened above; eyes dorsolateral, not visible from below; spiracle sinistral; anus dextral, tube opening not reaching margin of ventral fin.

Oral disk ventral, subterminal; two to four uninterrupted rows of papillae across border of lower lip; upper labial teeth II:3–3 in larvae without hindlimb buds, II:4–4 in those Stage I or older; lower labial teeth usually 1–1:II in Sarawak larvae, III in northeastern Bornean ones, though both counts occur in each sample; beaks finely serrated, narrowly edged with black.

Tail pointed, muscle weak; upper fin rising very little, deeper than muscle beyond proximal third, deeper than ventral fin throughout.

A dark spot on side of head anterior to eye; a second below and immediately before eye; a third spot below and behind eye; a black Y running back from eyes; body otherwise unmarked; tail unmarked, a dusting of separated, spaced melanophores. The coloration is generally darker in Sarawak larvae and may obscure the head markings though the anterior-most spot is usually visible.

Ecological notes.—*Rhacophorus pardalis* occurs in primary forest or logged areas in which at least low trees and tall shrubs are present. Of the Bornean frogs for which detailed information is available, 26 were caught deep in primary forest, three at the edge of primary forest, 38 in secondary growth or logged forests, and three at the edge of clearings in secondary growth. All were caught in low parts of drainages—along streams where the gradient is much reduced or absent, or in marshy areas.

The single foam nest identified (see above) was attached to low herbs at the edge of a small, isolated pool. Larvae were collected from pools in small, slowly flowing streams. Most adults were seen and collected on vegetation one to three meters above the surface of such pools.

Fifty eight Bornean specimens were caught within 100 meters of sea level, one at 200 meters, and fourteen between 400 and 500 meters.

Calling males having nuptial pads have been collected from May through August, and females containing enlarged ova in June and August. Larvae were also caught during the longer interval.

Geographic variation.—As noted above, Sarawak tadpoles are darker in general coloration than those from eastern Sabah and have more conspicuous lateral line organs. The innermost lower tooth row is continuous in 15 and interrupted in one larva from eastern Sabah; continuous in four and interrupted in nine from western Sabah; continuous in two and interrupted in five from the Baram basin of northern Sarawak; and interrupted in 10 from the Baleh basin of central Sarawak.

Frogs from the upper Baleh River basin are larger than those from other parts of Borneo. Males with vocal sacs from the Baleh measure 49.6–55.4 mm. (mean $=52.16\pm0.82$; $N=7$); 29 from Kalabakan, eastern Sabah, 38.7–46.5 (mean 42.33 ± 0.29); 10 from Bukit Kretam, eastern Sabah, 40.5–44.0 (mean $=42.38\pm0.45$); two from eastern Kalimantan, 40.8–41.0 mm. The web between the first two fingers usually reaches the distal edge of the subarticular on the second finger as a broad sheet in Bornean frogs. In those from the Baleh, however, full web extends somewhat beyond the tubercle in all but one specimen.

Bornean frogs have longer legs than those from the Philippines. The ratio of tibia to snout-vent is 0.474–0.594 (median 0.552) in 28 Bornean males and 0.486–0.535 (median 0.519) in 10 Philippine males; the difference between the two sets of ratios is statistically significant (Mann-Whitney U test applied; $P=0.002$). The relative head width is slightly but significantly larger (statistically) in the Philippine frogs. The head-width ratio varies from 0.318 to 0.350 (median 0.343) in 10 males from the Philippines and from 0.312 to 0.349 (median 0.334) in 26 from Borneo; using the Mann-Whitney test with these ratios yields $Z=2.49$, $P=0.012$.

Although the differences are difficult to measure and are probably affected by modes of preservation, the Bornean frogs consistently have wider fringes along the forearm and tarsus than do those from the Philippines.

Range.—Sumatra, Borneo, and the Philippine Islands.

SABAH: Beaufort District, Mengalong; Jesselton District, Jesselton, Kabayo; Kinabatangan District, Bukit Kretam; Sandakan District, Sandakan; Tawau District, Kalabakan; Labuan. SARAWAK: First Division, Santubong; Third Division, Baleh River near mouth of Putai River, headwaters of Baleh River, Mengiong River; Fourth Division, Long Akah, Long Lelang at headwaters of Akah River, Niah; Fifth Division, Pa Brayong. KALIMANTAN: Bluu on upper Mahakam, Kenepai Mountains, Long Petah, Merah, Pagat (van Kampen, 1923), Samarinda, Semberrah.

Rhacophorus rufipes[1] new species

Holotype.—Field Museum of Natural History 147699 an adult male collected five miles north of Labang, Fourth Division, Sarawak, December 3, 1963, by William Hosmer and James P. Bacon.

[1] So named because of the reddish webbing.

Diagnosis.—A small species of *Rhacophorus*, adult males less than 40 mm.; web of hand reaching disks of second, third, and fourth fingers; tympanum at least 1½ times width of disk of third finger; no rows of tubercles or dermal appendages on limbs or at vent; ventrally immaculate; webbing of hands and feet orange-red.

Description of holotype.—Body moderately slender; head wider than body; snout sharply pointed, projecting beyond lower law; canthus sharp, lores vertical, smooth; nostril closer to tip of snout than to eye; diameter of eye a little longer than eye-nostril distance; pupil horizontal; interorbital slightly wider than upper eyelid; tympanum three-fourths diameter of eye, 0.102 of snout-vent, 1.8 times disk of third finger, narrowly separated from eye, lower rim reaching lip; vomerine teeth in long, transverse groups beginning near anteromedian corners of choanae, gap between groups about half length of one group.

Tips of digits expanded into rounded disks, those of toes narrower than those of two outer fingers; first finger shorter than second, fourth almost as long as third; length of hand from wrist to tip of third finger equals distance from tip of snout to rear of eye; web reaching base of subarticular tubercle of first finger, distal edge of tubercle on inner edge of second finger, to disk on outer edge of second, to disk on both sides of third, and to disk of fourth; outer edge of fourth finger with a narrow fringe of skin; subarticular tubercle strong; small supernumerary tubercles on palm. All toes webbed to disks; a low oval, inner metatarsal tubercle; no outer metatarsal tubercle; small supernumerary tubercles on metatarsals.

Skin shagreened above, coarsely granular on abdomen and lower surfaces of hind limbs; a straight glandular ridge above tympanum from eye to a point above axilla; skin free of skull; arm and leg smooth, without dermal appendages except for two low tubercles at wrist; no dermal appendages or tubercles at vent.

Color (in life) pinkish brown above and on sides; back with dark speckling and five irregular, round spots; a thin white line from tip of snout along canthus and edge of eyelid; dorsal surface of limbs pink, rear of thigh and groin bright orange, throat and chest yellow-orange; webbing of hand and foot deep orange-red.

Measurements (mm.): snout-vent 37.1, head width 13.0, head length 14.8, diameter of tympanum 3.8, width 13.0, head length 14.8, diameter of tympanum 3.8, width of disk of third finger 2.1, tibia 20.1.

Round vocal sac openings near commissures of jaws; yellowish nuptial pad on dorsomedian aspect of first finger from base to above subarticular tubercle.

Paratypes.—FMNH 146555, 14700–05, from type locality; FMNH 144393, from Nanga Tekalit, Mengiong River, Third Division, Sarawak.

This series of two adult females and six adult males agrees with the holotype except for expected slight variations in body proportions and coloration. The statistics on body proportions include those of the holotype; all are given as thousandths of snout-vent.

Tibia 525–551 (median 536); head width 333–367 (median 347); head length 351–425 (median 384); tympanum of males 95–105 (median 101), of females 82–87; width of disk of third finger 52–64 (median 60).

All specimens have the same reddish brown ground color dorsally, orange flash surfaces on the hind leg, immaculate white ventral surfaces, orange-red webbing, and narrow light line on the canthus. Three have no dark dorsal marking on body or limbs. One has dark speckling dorsally but no crossbars on the limbs. The remainder have irregular round spots on the back and faint crossbars on the legs.

Secondary sex characters.—Both females have enlarged ova: they measure 49.5 and 50.4 mm. The males, all of which have nuptial pads and vocal sac openings, measure 34.3–38.7 mm. (mean 36.73 mm.). As indicated above, the tympanum is larger in males than in females. The sexes do not differ in other body proportions.

Ecological notes.—All specimens were caught in hilly, primary rain forest. Five of the males were calling in a group about 1.5–3.0 m. above ground.

Comparisons.—Eight species of Bornean *Rhacophorus* resemble *rufipes* in having well-developed webbing on the hand. *Rhacophorus fasciatus* and *R. harrissoni* are most similar to *rufipes;* these three species have the web reaching the disks of the three outer fingers, a short, straight, glandular ridge just above the tympanum from the eye to a point opposite the insertion of the fore limb, sharply pointed snouts (at least in males), and a minimum of dermal appendages on the limbs.

Rhacophorus harrissoni is larger (males 50–55 mm.) than *rufipes* and differs from the latter in having brown dorsal coloration, the disk of the third finger as wide as the tympanum, and the gap between groups of vomerine teeth equal to the length of one group (gap half

that length in *rufipes*). The two species have been collected at the same locality.

Rhacophorus fasciatus is slightly larger than *rufipes* though ranges of variation probably overlap. Examined adult males of *fasciatus* measure 42.9–44.5 mm. and the one adult female 52.5 mm. Corresponding ranges for *rufipes* are 34.3–38.7 and 49.5–50.4 mm. The striking differences between these two forms involve the tympanum, which is only two-thirds the diameter of the eye in *fasciatus* but about four-fifths the eye in *rufipes*. In males of the latter (seven examined) the diameter of the tympanum is 0.095–0.105 of snout-vent and at least 1½ times the width of the disk of the third finger. In *fasciatus* the tympanum is 0.069 of snout-vent in the one male for which I have exact measurements; in all three males seen the tympanum is subequal to the disk of the third finger or very slightly wider. *Rhacophorus fasciatus* lacks the light canthal line which is so characteristic of *rufipes*.

Differences between *rufipes* and other Bornean species are much more pronounced. *Rhacophorus nigropalmatus* is twice the size of *rufipes* (males 78–88 mm. *vs.* 38 mm.), is invariably green dorsally, and has a broad flap of skin on the lower arm. *Rhacophorus baluensis* and *pardalis* differ from *rufipes* in having dermal appendages on the limbs and the tympanum subequal to the disk of the third finger.

Rhacophorus acutirostris resembles *rufipes* in shape of the snout but has a curved supratympanic fold, the tympanum no wider than the disk of the third finger, dark spots on the rear of the thigh, and the second finger incompletely webbed.

Rhacophorus appendiculatus has less extensively webbed hands; none of the fingers is webbed to the disk. It also differs from *rufipes* in having dermal appendages on the limbs and at the vent.

Rhacophorus dulitensis and its extra-Bornean relatives, *reinwardti*, *prominanus*, and *bimaculatus*, differ from *rufipes* in having a dermal flap at the anus and dermal appendages of some sort on the limbs. *Rhacophorus reinwardti* and *bimaculatus* have dark spots on the webbing. The gap between groups of vomerine teeth equals the length of one group in *dulitensis*, whereas in *rufipes* the relative length of the gap is only half as large.

Other non-Bornean species having the outer fingers webbed to the disks are *robinsoni* Boulenger and *annamensis* Smith. Both of these species are readily distinguished from *rufipes* by their dark dorsal patterns (at least on the hind limbs) and by their relatively smaller tympana.

Range.—Known only from the Third and Fourth Divisions, Sarawak.

Rhacophorus larva A

Material examined.—Borneo 1 lot (FMNH).

The four larvae in this series are in what corresponds to *Rana pipiens* stage 25, at least with respect to total body form. However, the pattern of development is sufficiently different from those of *Rana pipiens* and most species of *Rhacophorus* that Shumway stages are not appropriate. One unfertilized egg was in the same foam nest.

Description.—Body ovate; tail lanceolate with rounded tip; in anterior two-thirds, caudal muscle deeper than either fin; both fins rise slightly in the distal third of tail; head projecting very little beyond the yolk mass; eyes well-developed; mouth open; lips thick but not expanded as in larvae of *Rhacophorus macrotis* or *otilophus*; no beaks, labial teeth, or papillae; olfactory pits present; no oral suckers; no sign of gills or operculum and hence no spiracle; no limb buds; gut not coiled; yolk mass highly vascularized superficially; vent median; dorsal surfaces gray with heavy dusting of chromatophores; density of chromatophores decreasing rapidly ventrad.

Head-plus-body lengths vary from 4.2 to 4.4 mm.; total lengths vary from 12.0 to 12.5 mm. The egg measures 3.8 mm. without membranes.

Relations.—The discovery of these larvae in a typical rhacophorid foam nest is reason for assigning them to this family group.

In some respects these larvae resemble those of *Rhacophorus hosei*, which probably are never free-swimming tadpoles; in other respects they resemble larvae of *R. macrotis* and *R. otilophus*, which are free-swimming. Like larval *hosei*, these larvae have a huge yolk mass and, associated with that, no coiling of the gut; both of these species of larvae lack oral suckers, gills, and operculum at a stage of optic and oral development (mouth open) when tadpoles of *macrotis* and *otilophus* have these structures. Larval *macrotis*, one day after hatching, still have oral suckers and several complete coils in the gut. Coiling of the gut in larval *otilophus* does not occur until four days after hatching, but before then the operculum has formed.

Unlike larval *hosei* but like larval *macrotis*, these larvae have slightly expanded lips.

Though limb development is not as precocious as in larval *hosei*, the large yolk mass and lack of oral suckers indicate that these larvae may have an abbreviated free-swimming stage or none at all.

Although the possibility that these larvae belong to a species of *Philautus* cannot be ignored, their resemblance to larvae of *Rhacophorus* species suggests they belong to that genus.

Ecological notes.—The foam mass was small (ca. 3×3 cm.) and attached to the underside of a leaf of a low herb growing on a rock at the edge of a small stream in primary forest.

Locality.—SARAWAK: First Division, Matang (FMNH 77574).

Rhacophorus larva B

Material examined.—Borneo 2 lots (FMNH). Larvae are in pre-limb bud stage and in Stages I–X.

Description.—Body ovate, flattened above and to a lesser extent below; eyes dorsolateral, not visible from below; diameter of eye one-half to two-thirds eye-nostril distance, less than half internarial distance, and about one-fourth interorbital; spiracle sinistral, non-tubular, in line with eye and root of hind limb bud, midway between eye and hind limb; anus dextral, opening not reaching margin of fin.

Mouth ventral, subterminal; beaks black-edged, smooth, upper one weakly convex at middle; lower lip with an inner continuous row of short, thick, closely-spaced papillae and an outer row of much longer, widely-spaced ones; short papillae confined to lateral corners of upper lip; teeth of upper lip I:4–4 (1 specimen), I:3–3 (3), or I:3–2 (1); those of lower lip 1–1:III (5).

Tail 0.58–0.61 of total length, moderately heavy, margins weakly convex, tapering gradually to rounded tip; dorsal fin beginning at end of body; caudal muscle deeper than either fin in proximal half.

Color (in life) purplish black on body and tail with yellowish brown spots on tail and side of body. In alcohol dark brown or slate gray.

Head-plus-body lengths (mm.) in these tadpoles are: pre-limb bud—12.0, 12.4; Stage I—13.3; Stage II—14.1; Stage X—22.0.

In the two from Sarawak, the row of long papillae is continuous across the lower lip. In the three from Sabah, the long papillae are confined to the lateral thirds of the lower lip.

Relations.—These tadpoles have characteristics of larval *Rhacophorus:* spiracle sinistral, vent dextral and not reaching edge of ventral fin, and papillae of upper lip confined to corners. They are not sufficiently advanced to have limb characteristics that can be compared to any species of adults.

Ecological notes.—Both series were collected in isolated pools on ridges in primary rain forest. Neither pool was part of a stream drainage system. Depth varied from two to seven cm. and the larger of the pools measured 2×5 meters. The bottoms consisted of fine silt. The remains of three empty foam nests were floating on the surface of the larger pool.

Localities.—SABAH: Tawau District, Kalabakan (FMNH 77562). SARAWAK: Third Division, Mengiong River (FMNH 137952).

Rhacophorus larva C

Material examined.—Borneo 3 lots (FMNH).

Description.—Body oval, a little depressed; eyes dorsal, not visible from below; diameter of eye one-half of eye-nostril distance, about one-third of interorbital width; spiracle sinistral, not tubular, opening below line between eye and root of hind limb, closer to eye; anus dextral, opening not reaching margin of fin.

Mouth ventral, subterminal; beaks black-edged, finely serrate; upper beak a smooth arc; papillae small, homogeneous, in a continuous double row across lower lip, confined to corners of upper lip; teeth of upper lip I:3–3 (5), I:3–4 (2), or I:4–4 (2), those of lower lip III.

Tail 0.62–0.68 of total length, weak, margins very weakly convex; fins deeper than caudal muscle in distal half.

Color of head, body, and tail dark gray, without light spots or mottling.

Total lengths (mm.): Stage V—25; Stage XVI—30; Stage XVIII—33, 37. Snout-vent of Stage XXII—10.5 mm.

Relations.—One lot was reared from a foam nest, which makes assignment to this family clear. Metamorphosing young from this lot have the outer fingers webbed to the disks, the web between first and second fingers reaching the subarticular tubercles, and no fringes on the lower arm or tarsus. The absence of these dermal fringes cannot be ascribed to immaturity as larvae of *dulitensis, nigropalmatus*, and *pardalis* (pp. 297, 323, 331) in similar stages have these structures. The only adults that resemble these larvae in these characters are those of *Rhacophorus fasciatus* and *R. harrissoni*.

The advanced larvae have dark crossbars on the limbs, which again illustrates their resemblance to *fasciatus* and *harrissoni* but does not help in assigning them to one species or the other. Twenty-two adults of *harrissoni* were collected at the localities where the lar-

vae were obtained, but only one *fasciatus*. This makes *harrissoni* the more likely parent.

Ecological notes.—The foam nest was found on the upper rim of a tree hole that contained water. The hole was 2.5 m. above ground. The second lot consists of a series of tadpoles collected in a hole of a tree buttress 1.3 m. above ground. Both sites were in primary rain forest.

Localities.—SARAWAK: Fourth Division, Labang, Sungei Pesu.

Philautus

KEY TO BORNEAN SPECIES.

1A. Outer fingers at least half webbed .... 4.
B. Outer fingers without web .... 2.

2A. Dorsal surfaces with many small spinose tubercles; a white line or series of spots along canthus .... *pictus*.
B. Dorsal surfaces smooth or with short ridges; never with white spots on canthus .... 3.

3A. Back dark brown with narrow light lines forming a network .... *amoenus*.
B. Dorsal coloration variable, but not as above .... *aurifasciatus*.

4A. Upper eyelid with a conical dermal projection (fig. 66) .... *gauni*.
B. Upper eyelid without a dermal projection .... *bimaculatus*.

Philautus amoenus Smith

Philautus amoenus Smith, 1931, Bull. Raffles Mus., no. 5, p. 18, pl. 1, fig. 3—Kamboranga, Mount Kina Balu, Sabah.

Material examined.—Borneo 2 (BM, holotype and paratype).

Taxonomic notes.—As noted by Smith (1931A), this form is similar to *mjobergi* (=*aurifasciatus*) but has a distinctive color pattern not found in the variable *aurifasciatus*. It also has very broadly sloping lores. Additional specimens from Kina Balu will probably show that *amoenus* is merely a color variant of *aurifasciatus*.

Description.—Body stocky; head large, broader than long; snout broadly rounded; canthus distinct; lores with a flat slope; eye large, diameter subequal to snout; tympanum distinct, about one-fourth eye diameter; no lingual papilla.

Fingers with disks, those of third and fourth fingers as wide as tympanum; fingers without web. Disks of toes smaller than those of outer fingers; first and second toes webbed to distal edges of subarticular tubercles on outer sides, third toe webbed to base of distal tubercle on outer edge and fifth toe to same level on inner edge, fourth

toe webbed to middle tubercle; metatarsals with many small tubercles.

Color (in alcohol) dark brown above with network of narrow light lines; below dusky; limbs with bold crossbars.

Adult male with vocal sac openings 23.8 mm., snout to vent; tibia 0.45 of snout-vent; head width 0.42.

Range.—Known only from the type locality on Mount Kina Balu.

Philautus aurifasciatus (Schlegel)

Hyla aurifasciatus Schlegel, 1837, Abbild. Amph., p. 27, pl. 9, fig. 4—Java.

Ixalus aurifasciatus Peters, 1872, Ann. Mus. Civ. Genova, **3**, p. 44.

Philautus aurifasciatus van Kampen, 1923, Amph. Indo-Austr. Arch., p. 276.

Ixalus acutirostris Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**, p. 32—eastern Mindanao.

Ixalus longicrus Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**, p. 88—Palawan.

Ixalus petersi Boulenger, 1900, Proc. Zool. Soc. London, **1900**, p. 185, pl. 17, fig. 3—Mounts Penrissen, Dulit, and Kina Balu, Borneo.

Philautus petersi van Kampen, *op. cit.*, p. 275; Smith, 1925, Sarawak Mus. Jour., **3**, p. 10, 34; 1931, Bull. Raffles Mus., no. 5, p. 20.

Philautus mjobergi Smith, 1925, *op. cit.*, p. 11, pl. 1, fig. 3—Mount Murud, Sarawak; 1931, *op. cit.*, p. 21.

Material examined.—Borneo 68 (46 BM, including types of *petersi* and *mjobergi*; 5 FMNH; 2 MCG; 6 MCZ; 4 SNM; 5 RMNH); Java 27 (14 AMNH; 1 CAS; 1 FMNH; 10 MCZ; 1 UMMZ); Palawan 37 (21 FMNH; 16 MCZ); Mindanao 45 (FMNH).

Taxonomic notes.—Van Kampen (1923, p. 276) doubted that the characters (tympanum size and coloration) used by Boulenger (1900) did distinguish *petersi* from *aurifasciatus,* but suggested that shape of the snout and position of the nostrils might. Smith (1925A) agreed with van Kampen and then described *mjobergi* as a distinct species. After examination of the types of *petersi* and *mjobergi* and comparison with the large series of Javan *aurifasciatus,* I conclude that only one highly variable species is involved. All of the British Museum *petersi* from Borneo have a conically tipped snout. The same shape characterizes Javan *aurifasciatus,* though some have rounded snouts. All specimens from Mount Murud and Kina Balu identified by Smith (1925A, 1931A) as *mjobergi* have rounded snouts and differ from those he identified as *petersi* from the same localities only in that character. If the frogs of those localities are considered as one species, two samples result showing the same variation in snout shape as the Javan series.

Smith (1925A) stated that *petersi* differed from *aurifasciatus* in length of leg, relative widths of interorbital and upper eyelid, and shape of snout. My examination of the present samples negates Smith's contention. The heel of *petersi* was said by Smith to reach beyond the tip of the snout; it does so in only one-third of the Bornean specimens (*mjobergi* and *petersi*). Leg length is not correlated with snout shape in these frogs (Table 41). The heel reaches beyond the snout in two-sevenths of the Javan series. The shape of the snout has been discussed above.

TABLE 41.—Frequency distribution of snout shape and leg length in Bornean *Philautus aurifasciatus*.

	Snout pointed	Snout rounded
Heel beyond snout	5	6
Heel not beyond snout	10	7

A conical lingual papilla is present in about three-fifths of the Bornean frogs but is not correlated with snout shape. It is present in 11 of 18 frogs having pointed snouts and in 11 of 19 having rounded snouts. None of the Javan frogs seen have lingual papillae.

The Philippine forms, *acutirostris* (Peters) and *longicrus* (Boulenger) from Mindanao and Palawan, respectively, show the same bewildering amount of individual variation (Inger, 1954A) over practically the same range as seen in *aurifasciatus* and are very likely the same species as the last. The Mindanao form consistently has a conically tipped snout, but has a more coarsely shagreened dorsal surface than the Bornean frogs. The Palawan form lacks the conical tip to the snout. The outer edge of the fifth metatarsal of Palawan *longicrus* often bears a narrow, crenulated fringe as in the Bornean specimens, contrary to my earlier statement (Inger, 1954A). A lingual papilla does not appear in the Philippine samples.

Description (based on Bornean specimens).—Body stocky (females) or slender (males); head large, usually broader than long, width 0.38–0.46 of snout-vent; snout obtusely pointed, tip with or without a conical projection; nostril nearer to tip of snout than to eye; canthi sharp, slightly convergent; lores oblique, weakly concave; eye diameter slightly shorter than snout length; interorbital wider than upper eyelid; tympanum obscured by skin, diameter less than half of eye.

Tips of fingers enlarged into round disks having circummarginal grooves; disk of third finger wider than tympanum; fingers without

web or a rudimentary web between first two fingers; metacarpals with many small tubercles. Tips of toes equal to or smaller than those of fingers; web reaching subarticular tubercles on outer edges of first two toes, the distal subarticular tubercle on the outer edge of third and inner edge of fifth, and middle tubercle on outer edge of fourth toe; in oval inner metatarsal tubercle; metatarsals with many small tubercles, including one in position of an outer metatarsal tubercle; tibia 0.50–0.62 of snout-vent.

Skin above with irregularly distributed tubercles and short ridges, coarsely granular below; a supratympanic fold from eye to axilla; frequently one or a pair of conical tubercles laterally in occipital region; a short, curved, dorsolateral ridge present or absent; heel with or without a small conical tubercle.

Color extremely variable above; a broad dark interorbital bar present or absent; back with a dark H- or X-shaped mark on a light background, or a broad, light, mid-dorsal band on a dark background, or light tan without markings; side of head dark, usually with a narrow light streak on supratympanic ridge, one from upper rear corner of eye through center of tympanum, one from lower rear corner of eye backward to mouth, and one from anterior corner of eye forward to mouth; limbs usually with dark crossbars; ventral surfaces cream-colored; throat usually spotted with brown, abdomen less often with similar spots.

Secondary sex characters.—Bornean females containing enlarged ova measure 23.9–33.3 mm. (mean 29.85 ± 0.69; $N = 13$). Males having vocal sacs measure 15.8–24.0 mm. (mean 21.78 ± 0.70; $N = 13$). The nuptial pad consists of a small yellowish patch on the dorsal surface of the first finger. The vocal sacs openings, located at the corners of the mouth, are circular or oval.

Ecological notes.—Bornean specimens for which data are available have the following altitudinal range:

Meters	below 1000	1200–1300	1500–2000	2100	3000
Specimens	6	5	16	20	5

The six for which details are available were caught in primary rain forest, one on the ground under a leaf and the others on vegetation between 0.6 and 3.7 m. above ground.

The ova are large (5 mm. according to Smith, 1925A; 3 mm. according to Smith, 1931A; ca. 2.5 mm. according to my measurements) and few in number (9 in one ovary). Probably the eggs are laid on land and the larvae are not free swimming.

TABLE 42.—Comparison of several samples of *Philautus aurifasciatus* in the ratio of head width to snout-vent (in thousandths).

Sample	No.	Range	Median
	Males		
Java	4	390–429	414
Borneo	7	408–463	434
Palawan	11	366–428	395
Mindanao	12	362–452	400
	H*=12.588	P=0.008	
	Females		
Java	4	360–433	401
Borneo	12	380–486	436
Palawan	2	380–393	386
Mindanao	7	372–429	418
	H*=5.100	P>0.10	

* Calculated by means of Kruskal-Wallis test.

Geographic variation.—The Bornean samples do not differ in any of the characters studied. As indicated in the *Taxonomic notes*, each population has the same wide range of variation in head shape, skin tuberculation, and leg length.

A lingual papilla appears in the majority of Bornean specimens but not in those from Java or the Philippines (see *Taxonomic notes*). Relative head width is larger in Bornean males than in those of other samples (Table 42); females do not differ significantly. Although coloration varies remarkably within some samples, the Mindanao series differs from the others in lacking the cruciform or H-shaped patterns.

Range.—From Thailand and Cambodia (Smith, 1930) to Java, Borneo, and the Philippine Islands. Taylor (1962) does not include this species in his list of the Thai fauna.

SABAH: Kota Belud District, Marei Parei; Ranau District, Kamborangah, Lumu Lumu, and Pakka on Mount Kina Balu. SARAWAK: First Division, Mount Penrissen; Fourth Division, Sungei Pesu; Fifth Division, Mount Murud. KALIMANTAN: Mount Kenepai, Liang Kubung, Mount Damas near Sambas, Mount Tilung.

Philautus bimaculatus (Peters)

Leptomantis bimaculatus Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**, p. 32—upper Agusan Valley, Mindanao.

Philautus bimaculatus Stejneger, 1905, Proc. U. S. Nat. Mus., **28**, p. 347; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 269; Inger, 1954, Jour. Washington Acad. Sci., **44**, p. 250.

Ixalus bimaculatus Boulenger, 1898, Proc. Zool. Soc. London, **1898**, p. 475.
Philautus zamboangensis Taylor, 1922, Philippine Jour. Sci., **21**, p. 173, pl. 1 fig. 7—Pasonanca, Mindanao.

Material examined.—Borneo 46 (1 BM; 1 Bogor Mus.; 43 FMNH; 1 USNM); Singapore 1 (FMNH); Thailand 2 (BM); Mindanao 3 (1 FMNH; 1 NHMW; 1 USNM).

Taxonomic notes.—Examination of additional specimens of *bimaculatus,* including some directly compared with the type by Smith (1930), confirms my previous opinion (Inger, 1954A) that *zamboangensis* Taylor is a synonym.

Description.—A medium-sized species of *Philautus,* adults 28–35 mm.; body slender; limbs long, slender; head longer than broad, width 0.30–0.34, length 0.33–0.36 of snout-vent; snout obtusely pointed, sloping backward to mouth in profile; nostril closer to tip of snout than to eye; canthi sharp, curved; lores sloping, not concave; eye diameter slightly shorter than snout length; interorbital equals upper eyelid; tympanum distinct, diameter about two-fifths that of eye.

Tips of fingers enlarged into round disks, that of third finger equal to diameter of tympanum; web between first two fingers a narrow fringe at bases; broad web reaching just beyond tubercle on outer edge of second finger, to basal tubercle on inner edge of third, beyond distal tubercle on outer edge of third and inner edge of fourth; metacarpals with small supernumerary tubercles. Disks of toes smaller than those of outer fingers; broad web reaching disks on outer edges of first three toes and on inner edge of fifth, to distal tubercle or beyond on both sides of fourth; a prominent, oval inner metatarsal tubercle; metatarsals with small, weak supernumerary tubercles; tibia 0.53–0.60 of snout-vent.

Skin smooth above, coarsely granular below; a curved supratympanic fold from eye to axilla; a narrow fringe of skin along outer edges of fourth finger and fifth toe; small whitish tubercles present or absent on outer edge of forearm; two or more white tubercles below vent.

Color sandy or dark brown above, a narrow, dark interorbital bar; three transverse, dark ovals on dorsum, one at occiput, one at the center of the back, and one over the sacrum; top of snout usually lighter than back; sides of head and body and anterior and posterior faces of thigh blackish brown; a conspicuous white or pink spot below eye; sides of body and anterior and posterior faces of thigh with light spots, bright blue in life; venter white, immaculate or dusted with brown.

Secondary sex characters.—Only one of the three adult females seen (33.8, 34.5, 42.7 mm.) falls outside the observed size range of adult males (28.3–34.9 mm., N = 9). Males have median vocal sacs having long slit-like openings in the floor of the mouth. The skin of the throat is rugose in males, smooth in females. Nuptial pads are absent, but a linea masculina is present at the dorsal edge of the obliquus muscle in males.

Ecological notes.—All but two of the Bornean specimens examined were caught in primary rain forest, 26 in flat, swampy forest and 16 in hill forest. One was caught in secondary growth. The rain forest frogs were mainly in vegetation 0.6–6 m. above the ground; one was found in an epiphyte. A pair in amplexus was caught at the entrance to a hole in a stream bank; other pairs were found as high as 3 m.

Only one Bornean specimen has been taken more than 150 meters above sea level. The exceptional specimen is from 1600 m. on Mount Kina Balu.

Geographic variation.—The few individuals seen show no geographic variation from one end of the range to the other.

Range.—From peninsular Thailand to Borneo and Mindanao.

SABAH: Kinabatangan District, Deramakot; Ranau District, Lumu Lumu on Mount Kina Balu. SARAWAK: Third Division, Mengiong River; Fourth Division, Labang, Sungei Pesu. KALIMANTAN: Mentawir.

Philautus gauni new species. Figure 66.

Holotype.—Field Museum of Natural History 136314, an adult female collected at Mengiong River, upper Baleh basin, Third Division, Sarawak on Oct. 9, 1962, by Bernard Greenberg, R. F. Inger, F. W. King, and Gaun Sureng.

Diagnosis.—A moderate-sized species of *Philautus* having the fourth finger webbed beyond the distal subarticular tubercle, a conical dermal tubercle in the middle of the upper eyelid, and the back smooth.

Description of holotype.—A medium-sized *Philautus*, snout-vent 35.7 mm.; head length and width equal, length 0.34, width 0.34 of snout-vent; snout broadly rounded, rounded in profile; nostril closer to tip of snout than to eye; canthi distinct, curved; lores sloping; diameter of eye longer than snout; pupil horizontal; interorbital equals upper eyelid; tympanum distinct, one-third diameter of eye; no vomerine teeth.

FIG. 66. *Philautus gauni*, paratype (FMNH 136315), 38 mm.

Tips of fingers enlarged into round disks, that of third finger about 1.5 times width of tympanum; web between first two fingers a narrow fringe reaching subarticular tubercles; broad web reaching disk on outer side of second finger, between subarticular tubercles on inner side of third, beyond distal tubercle on outer side of third, and disk on inner side of fourth; metacarpals with numerous small tubercles. Disks of toes smaller than those of fingers; broad web reaching disks on outer edges of first three toes and on inner edge of fifth toe, reaching distal subarticular tubercle of fourth toe; an oval inner metatarsal tubercle, no outer one; small supernumerary tubercles on metatarsals; tibia 0.51 of snout-vent.

Skin smooth above; a small conical tubercle in middle of upper eyelid; small tubercles at rictus; a weak supratympanic fold; throat

smooth; chest and abdominal region coarsely granular; a conical, dermal projection at tibio-tarsal joint; numerous infra-anal tubercles; a row of tubercles on edge of lower arm and tarsus; outer edge of fourth finger and fifth toe with narrow, smooth-edged fringe of skin.

Color (in life) light gray with faint, large, dark spots on back; dorsal surfaces of legs with dark crossbars; a large cream-colored spot below posterior half of eye; sides and ventrum white; anterior and posterior faces of thigh reddish orange; infra-anal area dark brown with cream-colored tubercles; web of fingers whitish, of toes brownish; iris pale brown, without network.

In alcohol hidden surfaces of legs pale yellow.

Paratypes.—FMNH 136315, 136320, 137981–88, 139343–46. Ten adult males and four adult females, collected within a radius of 10 kilometers from the type locality in the same area of rain forest, between Oct. 9, 1962, and March 22, 1963.

The paratypes agree with the holotype in all characters except those mentioned immediately. The webbing of the fourth finger may reach just beyond the distal tubercle or all the way to the disk. Two of the paratypes lack white tubercles on the lower arm and tarsus. The white infraorbital spot is absent in one paratype and only faintly indicated in another. The spotting on the back is variable, but all specimens have a dark interscapular spot that may be oval, circular, or triangular.

Snout-vent of females 35.6–38.4 mm. (mean 36.7), of males 25.5–30.2 mm. (mean 27.36); tibia 0.51–0.58 of snout-vent.

Males have median subgular vocal sacs but no nuptial pads or asperities.

Remarks.—These frogs were caught at night 0.7–8.0 meters above the ground in small trees in primary rain forest along small tributaries of the Mengiong River.

The species is named after a collector for the Sarawak Museum, Mr. Gaun Sureng, who accompanied me on three successive expeditions and who caught many of the poorly known forms obtained on those occasions.

Comparisons.—Only four species of *Philautus* of the Indo-Malayan region have well-developed webbing on the hand: *P. montanus* Taylor—Sulu Islands; *P. horridus* (Boulenger)—Malaya, Thailand, and Mentawei Islands; *P. bimaculatus* (Peters)—Malaya, Borneo, and Mindanao; and *P. gauni*.

Philautus montanus has less extensive webbing (outer fingers webbed only to basal subarticular tubercles), a relatively longer head (longer than broad), a smaller eye (diameter equal to eye-nostril distance), a larger tympanum (equal to half diameter of eye), and smaller finger disks (two-thirds diameter of tympanum) than *P. gauni*.

Philautus horridus differs from *gauni* in having warty dorsal skin, the head longer than broad, the tympanum subequal to the eye, and the belly spotted with black. Apparently, it also has less extensive webbing between the outer fingers, as Boulenger (1903, 1912) said the fingers were "half-webbed."

Philautus bimaculatus usually has a cream-colored spot below the eye and large dark spots on the back, both conspicuous elements in the coloration of *gauni*. But *bimaculatus* has black sides and thighs set with bluish white spots, whereas in *gauni* the sides are white and the flash surfaces of the thighs are uniform reddish orange. Unlike *gauni*, *bimaculatus* has no dermal projections on the upper eyelid or at the tibio-tarsal joint. In general, *gauni* is stockier than *bimaculatus*. The snout of *gauni* is rounded to truncate, that of *bimaculatus* distinctly pointed. The head of *gauni* is shorter (0.32–0.34 of snout-vent) than that of *bimaculatus* (0.34–0.36, N = 6). The leg of *bimaculatus* is longer, the tibio-tarsal joint reaching the tip of the snout or beyond and the tibia 0.53–0.60 of snout-vent. In *gauni* the heel does not reach beyond the eye and the tibia is 0.51–0.52 of snout-vent. Finally, the fingers in *bimaculatus* are not webbed as fully as in *gauni;* the third finger of *bimaculatus* is not webbed to the disk. The two species are sympatric; six specimens of *bimaculatus* (FMNH 136316, 137989–92, 139347) were caught in the same area of rain forest as the *gauni* series.

Range.—Known only from the Third Division, Sarawak.

Philautus pictus pictus (Peters)

Ixalus pictus Peters, 1871, Monatsber. Akad. Wiss. Berlin, **1871**, p. 580—Sarawak; Ann. Mus. Civico Genova, **3**, p. 44, pl. 6, fig. 2.

Philautus pictus van Kampen, 1923, Amph. Indo-Austr. Arch., p. 269; Smith, 1931, Bull. Raffles Mus., no. 5, p. 19; Inger, 1956, Fieldiana, Zool., **34**, p. 422.

Rhacophorus anodon van Kampen, 1907, *in* Weber, Zool. Ergebn. Riese Niederl. Ost-Indien, **4**, p. 400, pl. 16, fig. 2—Kaju Tanam, Sumatra.

Philautus anodon van Kampen, 1923, *op. cit.*, p. 271, fig. 29.

Material examined.—Borneo 56 (4 BM; 39 FMNH; 1 MCG, holotype of *pictus;* 1 MCZ; 11 SM); Sumatra 2 (MCZ); Malaya 2 (1 BM; 1 FMNH).

Taxonomic notes.—Smith (1931A) correctly assigned *anodon* (van Kampen) to the synonymy of *pictus* and stated that the only difference between *pictus* and *margaritifer* (Boulenger) lay in the extent of webbing. After examining the types of *pictus* and *flavosignatus* (Boettger), and a topotype of *margaritifer* (BM 1885.12.31.35) identified by Boulenger, I am convinced that *margaritifer* and *flavosignatus* are identical (*margaritifer* having priority) and that *margaritifer* is distinct from *pictus* only at the subspecific level as suggested by Smith. The two forms agree in the remarkable skin ornamentation, in the distinctive color pattern, in the fusion of the skin and skull, and in having reduced webbing. The Javan form, *pictus margaritifer*, is larger (males to 45 mm., largest of nine *p. pictus* 33 mm.) and has spinose tubercles across the throat, which is smooth in *p. pictus*. The web of *p. pictus* reaches the middle subarticular tubercle or midway between the basal and middle tubercle of the fourth toe; in *p. margaritifer* the web does not extend beyond the basal tubercle of the fourth toe. Similar differences apply to the webbing of all toes.

Description.—Size moderate, 30–35 mm.; body and limbs slender; head longer than broad, width 0.32–0.36, length 0.39–0.42 of snout-vent; snout obtusely pointed, vertically truncate in profile or sloping backward to mouth; nostril twice as far from eye as from tip of snout; canthi distinct; lores vertical or nearly so, feebly concave; eye diameter equals eye-nostril distance; interorbital wider than upper eyelid; tympanum distinct, about two-thirds eye diameter.

Tips of fingers enlarged into round or oval disks, that of third finger not as wide as tympanum; fingers without webbing; supernumerary metacarpal tubercles present. Disks of toes smaller than those of outer fingers; broad webbing reaching distal edge of subarticular tubercle on outer edge of first toe, between tubercle and disk on outer edge of second, between tubercles or to center of distal tubercle of third toe, between basal and middle tubercle or to middle tubercle of fourth toe, and between tubercles of fifth toe; an oval inner metatarsal tubercle; numerous small supernumerary metatarsal tubercles; tibia 0.53–0.61 of snout-vent.

Skin of all dorsal surfaces with spinose tubercles; limbs with similar tubercles; throat smooth, chest rugose, abdomen coarsely granular; skin of head fused to skull; no supratympanic fold; two to six whitish tubercles above vent and a similar group below it.

Color (in life) dark chocolate or cinnamon brown above; small whitish spots scattered over back; a row of similar spots along canthus and edge of upper eyelid; a longitudinal light spot on shoulder;

white spots on limbs, usually on tubercles, often forming transverse rows; dorsal surfaces of disks of first two fingers white, those of outer fingers brown in center and white at outer corners; ventral surfaces white or ivory; iris bi-colored, chocolate brown in lower half, white in upper half.

In alcohol brown of dorsum usually fades to lighter tone.

Secondary sex characters.—Females are slightly but statistically larger than males. Six adult (judging by the enlargement of oviducts) females from various parts of the range measure 31.5–34.2 mm. (mean 32.85 ± 0.46); eight males having nuptial pads measure 30.0–33.0 mm. (mean 31.25 ± 0.38). The difference between the means is statistically significant ($t = 2.698$; $P = 0.02$).

Males lack vocal sacs and lineae masculinae. A yellowish nuptial pad occupies an oval area in the center of the dorsal surface of the first finger.

Larvae.—A series collected at one site include large pre-limb bud stages and one example reared to early stages of metamorphosis. The last has the distinctive color pattern of adult *P. pictus*, as well as the characteristic dorsal spinules. Another set includes one metamorphosing young that has the bases of three lower rows of labial teeth. A description of larvae in the early stages of development follows.

Body oval, depressed, width about seven-eighths of length; eyes dorsal, interocular width about one-fourth of body width, diameter of eye 0.04 of head-plus-body, one-third of eye-nostril distance and one-fourth of interorbital; spiracle ventrolateral, closer to root of tail than to snout; vent median.

Mouth ventral, subterminal; beaks with wide black edge, serrate; lower lip with two continuous rows of papillae; teeth II:3–3/III in five specimens.

Tail 0.55–0.62 of total length, heavy; margins of fins subparallel; tip rounded; caudal muscle deeper than fins in proximal half.

Color of body and caudal muscle purplish brown, body paler below; fins dark, uniform.

Ecological notes.—All 41 Bornean specimens for which detailed information is available were caught in rain forest, about evenly divided between swamp forest and better drained areas. They were caught between ground level and 1.5 m., though only two were actually on the ground. Four were found in a water-filled tree hole one meter above ground.

Two sets of eggs were found on the walls of water-containing tree holes 5–10 cm. above the water. Each egg was surrounded by a large amount of gelatin which permitted each to hang down from the wall. Several of these eggs were brought back to the field lab where several developed to metamorphosis. The tree holes were 1.3–2.6 m. above ground. As noted above, adults of this species have been found in watery tree holes.

With one exception, the known Bornean specimens were caught within 200 meters of sea level. The exceptional specimen was taken at 1600 meters on Mount Kina Balu (Smith, 1931A). Boulenger (1912) recorded *pictus* from 800 and 1200 meters in Malaya.

Geographic variation.—Frogs from Malaya and Sumatra are remarkably like those from Borneo. Within this series of samples no geographic variation was observed. The divergence of the Javan population, *pictus margaritifer* is described above under *Taxonomic notes.*

Range.—Malaya, Singapore, Sumatra, and Borneo.

SABAH: Kinabatangan District, Bukit Kretam, Deramakot; Labuk District, Paitan; Ranau District, Lumu Lumu on Mount Kina Balu. SARAWAK: First Division, Kuching; Third Division, Mengiong River; Fourth Division, Akah River, Niah, Long Sinei, Sungei Pesu. KALIMANTAN: Barabei.

CAECILIIDAE

Ichthyophis Fitzinger

Two species of *Ichthyophis* have been known from Borneo, the unicolored *monochrous* (Bleeker) and the striped *glutinosus* (Linnaeus). Taylor (1960) has added a third form, *dulitensis,* which is said to be distinguished from *monochrous* by having more skin folds, a large light spot on the throat, a larger head, and six more vertebrae. Taylor had examined only one putative *dulitensis* and made no attempt to distinguish between individual and interspecific variation. A Bornean specimen (FMNH 67349) borrowed by Taylor but not mentioned in his paper lacks stripes as do *monochrous* and *dulitensis,* but it has a small yellow spot on the throat and is thus intermediate between them in color.

The difference in number of skin annuli (according to Taylor "approximately 247" in the type of *monochrous* and 313 in the single *dulitensis*) may also represent intraspecific variation. Taylor gave 302–344 as the range of variation in this character in eight *I. mindanaoensis* from one locality (Taylor, 1960, p. 73). This particular character is notoriously unreliable in *Ichthyophis* because of extraneous sources of error, such as peculiarities of fixation and method of counting primary and secondary rings. Taylor (p. 55) noted that the century old type of *monochrous* was dehydrated and the back had the skin folds loosened. The number of vertebrae is the only safe measure of segmentation in *Ichthyophis,* and in this count the holotype of *dulitensis* (114) is very similar to the type of *monochrous* (108).

Without better evidence than provided by Taylor, *dulitensis* should not be recognized as distinct from *monochrous.*

Taylor (1960) is probably correct in his belief that more than two species of *Ichthyophis* exist in the wide geographic range, which extends from Ceylon to the Philippine Islands. However, his publication is rather abstruse for several reasons. For one thing, the kinds of variation to which the characters used are subject are not analyzed. This failure makes a reasonable evaluation of the 18 new species Taylor describes difficult as 10 of them are based on single specimens.

My comments on *I. dulitensis* above show what kinds of difficulties are involved.

The second major defect of Taylor's paper is the failure to deal with the identification of *I. glutinosus*, the type species. After mentioning *glutinosus* in the introduction of the paper and quoting Linnaeus' description, Taylor does not refer a single caecilian to this species. Are any of the five striped forms described as new by Taylor identical to *glutinosus*, which is also striped? Three of these new forms are based on single specimens: *paucidentulus*, *nigroflavus*, and *paucisulcus*. A fourth, *kohtaoensis*, is based on two transformed specimens and the fifth, *supachaii*, on six. According to Taylor, the first two species lack splenial teeth, whereas the last three have from 13–18 splenial teeth on each side.

Probably two distinct groups are involved, but which is most similar to *glutinosus* is not indicated by Taylor. All but two of the 46 Bornean caecilians I have studied are striped. These striped caecilians have four or five splenial teeth as larvae, but none after metamorphosis, thus recalling the dental change at metamorphosis of some salamanders (Parker and Dunn, 1964). Vertebral counts in one local sample vary from 105 to 132 (10 specimens) and span the counts Taylor gives for *paucidentulus* (122) and *nigroflavus* (123) (Taylor, 1960, pp. 49, 101), which also lack splenial teeth. I suspect that the Bornean striped caecilians are conspecific with *paucidentulus* (type locality Sumatra) and *nigroflavus* (type locality Malaya).

Taylor (p. 51) believes that *paucidentulus* differs from *glutinosus* in the absence of splenial teeth. Taylor does not explain how he knows that *glutinosus* has splenial teeth. As no good reason has been presented for separating the striped Malayan, Sumatran, and Bornean caecilians from *glutinosus*, I am referring the Bornean ones to the Linnaean species.

Ichthyophis glutinosus (Linnaeus)

Caecilia glutinosa Linnaeus, 1758, Syst. Nat., 10th ed., p. 229—"in Indiis."

Ichthyophis glutinosus Gray, 1850, Cat. Amph. Brit. Mus., p. 60; Boulenger, 1882, Cat. Batr. Grad. Brit Mus., p. 89, pl. 4, fig. 2; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 2, fig. 1.

Material examined.—Borneo 8+36 larvae (6+larvae FMNH; 2 SM).

Taxonomic notes.—See preceding pages.

Description.—Head as wide posteriorly as body; snout rounded; eyes small, visible through skin; tentacular opening at lip, much closer to eye than to nostril; maxillary teeth 23–28, mandibular teeth 21–22; vomeropalatal tooth row as long as maxillary row; splenial with five teeth in larvae, none in metamorphosed caecilians; vertebrae 105–132; tail with three to six annuli; total length of transformed individuals 169–400 mm.

Color (in life) black with a bright yellow lateral stripe; stripe varying in width. In alcohol a light spot surrounding vent and tentacular opening; a narrow light ring around eye.

Larvae.—Total length 57–232 mm.; head depressed, length measured to spiracle 0.061–0.094 of total length; caudal fin distinct but not higher than body.

Ecological notes.—Larvae are found in small streams (ca. 2–10 m. wide) having clear water, moderate current, and sand, gravel, and rock bottoms. Most of the larvae examined were caught in such streams in primary rain forest, but 10 were obtained in streams flowing through secondary growth. The six metamorphosed individuals for which I have data were caught under leaves or logs in primary forest.

Most specimens have been collected within 300 meters of sea level, but one specimen (FMNH 130926) was caught at 470 m. and one (SM unnumbered) on the Kelabit plateau (ca. 1000–1150 m.).

Range.—Because of the taxonomic confusion surrounding the name *I. glutinosus*, a statement of range is meaningless at this point. The localities that follow, however, do, in my opinion, refer to a single species.

SABAH: Kinabatangan District, Bukit Kretam; Ranau District, Sungei Matukungan; Tawau District, Kalabakan. SARAWAK: First Division, Kuching, Matang (Boulenger, 1882); Third Division, Baleh River near mouth of Putai River, Mengiong River; Fourth Division, Kelabit Plateau.

Ichthyophis monochrous Bleeker

Ichthyophis monochrous Bleeker, 1858, Nat. Tijds. Ned. Indie, **16**, p. 188—Singkawang, Borneo; Boulenger, 1882, Cat. Batr. Grad. Brit. Mus., p. 91, pl. 4, fig. 1; 1892, Proc. Zool. Soc. London, **1892**, p. 508; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 3; Taylor, 1960, Univ. Kansas Sci. Bull., **40**, p. 51, figs. 3–4.

Ichthyophis dulitensis Taylor, 1960, *ibid.*, p. 58, figs. 7–8—Mount Dulit, Sarawak.

Material examined.—Borneo 2 (FMNH).

Taxonomic notes.—See above, p. 353.

Description.—Head as wide as body; snout rounded; eyes small, visible through skin; tentacular opening at lip, much closer to eye than to nostril; maxillary-premaxillary teeth 18–25, vomeropalatal teeth 19–21, mandibular teeth 19–23, splenial teeth 2–4; vertebrae 108–114; tail with 4–6 annuli; total length of transformed individual 209 mm.

Color purplish black; metamorphosed caecilian with small, diffuse yellow spot on throat.

Larva.—Total length 192 mm.; head depressed, length to spiracle 0.063 of total length; caudal fin distinct.

Ecological notes.—The larva examined was caught in a stream at 580 meters above sea level. The holotype and one additional specimen (FMNH 67349) were collected near sea level.

Range.—Identified with relative certainty only from Borneo.

SABAH: Ranau District, Mamut. SARAWAK: Third Division, Mount Dulit (Boulenger, 1892); Fifth Division, Lawas. KALIMANTAN: Singkawang (Bleeker, 1858).

ZOOGEOGRAPHY

Introduction

Discussions of the distributions of animals are no better than the reliability of the taxonomy and the negative evidence necessarily involved.

How completely is the amphibian fauna of Borneo known at least with respect to occurrence of species? Van Kampen (1923) recorded 66 species, allowing for subsequent synonymies. Smith in 1925 added two species to the list and two more in 1931. Within the past 10 years and including this publication, 20 more species have been recorded. These last additions represent a gain in the last three decades of about 25 per cent. Field work in the last 13 years has been intense, involving active parties from the Sarawak Museum, the Geological Survey of Borneo, and Field Museum of Natural History.

It is unlikely that the next 30 years will see a comparable addition. New species certainly remain to be discovered. In this monograph, six species of tadpoles of the genus *Amolops* are described, whereas only three species of adults are known at this time. With better collecting of the tree crown stratum in the rain forests, unrecorded arboreal species may be found. The addition of five to 10 species (ca. 5 to 12 per cent increase), however, will probably not affect the faunal composition significantly.

Roughly three-fifths of the Bornean species are now known from other areas. Determination of the ranges of these non-endemic species depends on collecting effort in extra-Bornean territories. The faunas of the Philippine Islands, Malaya, Thailand, and Indo-China are reasonably well-known. The field work of R. Bourret, M. A. Smith, E. H. Taylor, W. C. Brown, A. Alcala, the Philippine Zoological Expedition of Field Museum of Natural History, and numerous resident naturalists in Malaya have made it possible to describe the amphibian faunas of those areas with assurance. Similarly, Java has been subject to thorough herpetological exploration (Mertens, 1957). That is not to say that we are aware of all of the species occurring in those areas, for as late as 1957 Mertens reported a well-

known Malaysian species (*Kalophrynus pleurostigma*) from Java for the first time. Nevertheless, we may estimate that currently the species lists from those areas are about 80 to 90 per cent complete.

Our knowledge of the Sumatran fauna is far less satisfactory. On the basis of its large area, its topographic variation, its originally extensive cover of rain forest, and its Pleistocene connections with Borneo and Malaya (de Beaufort, 1951), one would expect Sumatra to have approximately as many species of amphibians as Malaya and Borneo. That Sumatra has relatively few species (Table 43) most likely reflects lack of intensive collecting rather than a real impoverishment of the fauna. In the discussion that follows, the absence of Bornean or Malayan groups from Sumatra cannot be treated as reliable negative evidence.

Most herpetological collecting in Borneo has been carried out in Sarawak and Sabah. Collecting effort has been well spread in Sarawak, but concentrated on Mount Kina Balu in western Sabah and in the lowlands in eastern Sabah. Analysis of the distribution of amphibians within Borneo at this time is more likely to reflect the distribution of collectors instead of frogs. For this reason, geographic distribution within Borneo will not be discussed.

The caecilians are omitted from this discussion of zoogeography because the taxonomic muddle surrounding the genus *Ichthyophis* (see p. 353) makes reasonably accurate statements of distributions impossible.

Geographic Relations of the Bornean Amphibians

Most of the non-endemic Bornean amphibians (total 51 species, see data in Table 44) reach Sumatra (40 species) and Malaya (37), about half as many reach the Philippine Islands (22) and Java (22), and still fewer reach Celebes (10) and Thailand north of the Isthmus of Kra (15). The last 15 species include all of those reaching Burma (11), Indo-China as defined in Table 43 (10), and China (8). The species ranging farthest north is *Rana limnocharis,* said to reach 36° N by Pope and Boring (1940). Towards the southeast only nine Bornean species range into the Lesser Sunda Islands.

Thus, the distributional relations of its amphibians confirm the close association of Borneo with the Malaya Peninsula, Sumatra, Java, and the southern Philippine Islands often mentioned in the literature (*vide* Darlington, 1957, p. 437).

The 91 species of Bornean amphibians represent five families (Tables 43 and 44) that are widely distributed in the Oriental Region.

TABLE 43.—Taxonomic distribution of the species of amphibians from certain parts of the Oriental Region.

	Indo-China[1]	Thailand[2]	Malaya[3]	Borneo	Sumatra[4]	Java[4]
Discoglossidae	1	—	—	—	—	—
Pelobatidae	7	7	8	6	2	2
Bufonidae	6	3	11	24	11	6
Hylidae	2	1	—	—	—	2[5]
Microhylidae	11	13	16	15	10	4
Ranidae	34	29	32	26	18	13
Rhacophoridae	17	11	13	20	18	9
Total species	78	64	80	91	59	36
Area (mi.^{2})	272,000	167,000	81,000	282,000	163,000	51,000

[1] Data from Bourret (1941). Indo-China as used in this table includes Laos, Cambodia, and North and South Viet Nam.

[2] Data from Taylor (1962). Includes only area and species occurring north of Isthmus of Kra.

[3] Data from Smith (1930) and Taylor (1962). Includes area and species occurring south of Isthmus of Kra.

[4] Data from van Kampen (1923), Mertens (1934, 1957), Parker (1934), Wolf (1936), and preceding pages of this monograph.

[5] Almost certainly recent introductions by man (Mertens, 1930).

The probable origins and distributions of the groups occurring in Borneo are discussed below. For the purposes of this paper "Malaysia" is used for the geographic area comprising the Malay Peninsula south of 12° N, the Greater Sunda Islands, and the southern Philippine Islands. The term "Indochinese area" or region refers to the area including Thailand north of 12°, Laos, Cambodia, and North and South Viet Nam.

Distributional data are based on the authors listed in Table 43 or are given in the taxonomic portion of this paper. Ranges of the species found in Borneo are given in Table 44.

PELOBATIDAE: Three genera appear in Borneo (see p. 17).

Nesobia—One species is known from Borneo and one from the Natuna Islands. The genus is probably autochthonous in Malaysia.

Megophrys—Two species are endemic to Malaysia. One of them, *baluensis*, is confined to Borneo and is probably autochthonous there, as it seems to be a derivative of *M. monticola*. The genus has its main center of speciation in the Indochinese and Burmese areas.

Leptobrachium—One species, *gracilis*, is endemic to Borneo and other parts of Malaysia; it may be autochthonous in Malaysia. A second species, *nigrops*, is known only from the Malay Peninsula and Borneo. A third species, *hasselti*, is widely distributed in Southeast Asia. More species occur in Indochina and China than in Malaysia.

TABLE 44.—List of species of frogs occurring in Borneo.

		Distribution outside of Borneo
mal[1]	*Leptobrachium gracilis*	M
shared	*L. hasselti*	S, J, M, T, I, P
mal	*L. nigrops*	M
mal	*Megophrys monticola*	S, J, M, P
	M. baluensis	
	Nesobia mjobergi	
mal	*Bufo biporcatus*	S, J, Ls, P
mal	*B. quadriporcatus*	S, M
shared	*B. melanostictus*	S, J, M, T, I, B, Ls
trans-m	*B. asper*	S, J, M, B, T
mal	*B. juxtasper*	S
mal	*Cacophryne borbonica*	S, J, M
	Pelophryne guentheri	
mal	*P. breviceps*	S, M, P
	P. macrotis	
	P. misera	
	Pedostibes everetti	
	P. maculatus	
trans-m	*P. hosei*	S, M, T
	P. rugosus	
	Ansonia albomaculata	
	A. fuliginea	
	A. guibei	
	A. hanitschi	
	A. latidisca	
	A. leptopus	
	A. longidigita	
	A. minuta	
	A. platysoma	
mal	*Pseudobufo subasper*	S, M
	Calluella brooksi	
	C. smithi	
trans-m	*Kaloula pulchra*	S, M, T, I, B, C
mal	*K. baleata*	S, J, M, C, P, Ls
	Kalophrynus heterochirus	
	K. intermedius	
shared	*K. pleurostigma*	S, J, M, T, I, B, P
mal	*K. punctatus*[3]	
	K. subterrestris	
mal	*Chaperina fusca*	M, P
	Metaphrynella sundana	
	Gastrophrynoides borneensis	
mal	*Microhyla annectens*	M
trans-m	*M. berdmorei*	S, T, I, B
	M. borneensis	
shared	*Ooeidozyga laevis*	S, J, M, T, B, Ls, C, P
	O. baluensis	
	Micrixalus borneensis	
	Amolops cavitympanum	
mal	*A. jerboa*	S, J, M

TABLE 44.—List of species of frogs occurring in Borneo (*Continued*)

		Distribution outside of Borneo[2]
	A. kinabaluensis	
mal	*Staurois natator*	P
	S. tuberilinguis	
	S. latopalmatus	
mal	*Rana baramica*	M
mal	*R. blythi*	S, M
trans-m	*R. cancrivora*	S, J, M, T, I, Ls, C, P
mal	*R. chalconota*	S, J, M, C
shared	*R. erythraea*	S, J, M, T, I, B, C, P
mal	*R. glandulosa*	S, M
trans-m	*R. hosei*	S, J, M, T
	R. ibanorum	
shared	*R. kuhli*	S, J, M, T, I, B, C
trans-i	*R. laticeps*	M, T
shared	*R. limnocharis*	S, J, M, T, I, B, Ls, P
mal	*R. luctuosa*	M
mal	*R. macrodon*	S, J, M
mal	*R. microdisca*	S, J, Ls, C, P
mal	*R. nicobariensis*	S, J, M, P
	R. paramacrodon	
mal	*R. signata*	S, M, P
mal	*Rhacophorus acutirostris*	S
mal	*R. appendiculatus*	S, M, P
	R. baluensis	
mal	*R. colletti*	S, M
mal	*R. dulitensis*	S
mal	*R. everetti*	P
	R. fasciatus	
	R. harrissoni	
	R. hosei	
shared	*R. leucomystax*	S, J, M, T, I, B, Ls, C, P
mal	*R. macrotis*	S, P
mal	*R. nigropalmatus*	S, M
mal	*R. otilophus*	S
mal	*R. pardalis*	S, P
	R. rufipes	
	Philautus amoenus	
mal	*P. aurifasciatus*	S, J, P
mal	*P. bimaculatus*	M, P
	P. gauni	
mal	*P. pictus*	S, M

[1] Prefixes are explained on p. 367. Endemic Bornean species have no prefixes.

[2] S=Sumatra; J=Java; M=Malay Peninsula to Isthmus of Kra; T=Thailand north of Isthmus of Kra; I=Indo-China (as defined in Table 43); B=Burma; Ls=Lesser Sundas; C=Celebes; P=Philippine Islands.

[3] Only extra-Bornean locality is Mentawei Islands.

Malaysia does not seem to have been an important center of development of this family (see p. 359). Only two stocks, *Megophrys-Nesobia* and *Leptobrachium*, have become established there and these have undergone only limited speciation. By contrast, southern China and the northern portions of Burma and the Indochinese area, have more species of those two stocks as well as two additional genera, *Scutiger* and *Oreolalax* (Myers and Leviton, 1962). The number of species of *Megophrys* and *Leptobrachium* decreases regularly southward from northern Burma and Indochina. There is no evidence of retreat from a former center in Malaysia; there are no disjunct ranges or relict distribution.

BUFONIDAE: This family has undergone a remarkable Malaysian radiation that, so far as now known, seems to have been centered on Borneo (p. 53).

Ansonia—Nine species are known from Borneo, two from Mindanao, two from the Malay Peninsula, and one from southern India. The genus has not been reported from Sumatra where it must surely occur.

Cacophryne—This genus is almost certainly autochthonous in Malaysia. The two known species are confined to this area, one widely distributed and one (*cruentata*) confined to Java.

Pedostibes—Four species occur in Borneo, one (*hosei*) in Sumatra, Malaya, and Thailand, one (*kempi*) in Assam, and one (*tuberculosus*) in southern India. Probably additional species will be found in Sumatra.

Pelophryne—The genus is autochthonous in Malaysia. The taxonomy is still not clear. As a result of treatment in this paper, which some may object to as "lumping," the number of species has been reduced. However, the effect of my taxonomic decisions has been to reduce only the number of species known from Borneo. At present, four species are recorded from Borneo, three from the southern Philippine Islands, and one (*brevipes*) from Sumatra and the Malay Peninsula. Probably more species of these small, cryptic toads will be discovered in Sumatra and, possibly, Malaya.

Pseudobufo—This monotypic, specialized genus is autochthonous in Malaysia.

Bufo—Most of the Bornean species are endemic to Malaysia. The same is true of the species occurring in Java and Sumatra. One species, *melanostictus*, is widespread in the Oriental Region including Malaysia. Another species, *asper*, though primarily Malaysian in distribution, occurs in southern Burma and Thailand.

Only one additional bufonid genus, *Ophryphryne*, occurs in the Oriental Region; it is known only from Annam and Tonkin. Thus, of the seven genera in the Oriental Region, three are confined to Malaysia, two have their centers of speciation in Malaysia, one is cosmopolitan, and one does not occur in Malaysia.

MICROHYLIDAE: Seven genera are known from Borneo.

Calluella—Three species are endemic in Malaysia, two in Borneo and one in Sumatra (*C. volzi*). A third species, *guttulata*, mainly Indochinese in distribution, occurs within the northern edge of Malaysia. A fourth species lives in China (Liu, 1950).

Kaloula—Three species are endemic in the Philippine Islands (Inger, 1954A). Of the two other species found in Malaysia, one, *baleata*, is confined to Malaysia and islands to the east and is probably autochthonous here. The second, *pulchra*, is widely distributed from China to the tip of the Malay Peninsula and appears at scattered localities in the East Indies. Five species are endemic to China.

Kalophrynus—Six of the seven species of this genus are endemic to Malaysia. The seventh, *pleurostigma*, occurs throughout Malaysia and the Indochinese area and reaches southern China.

Chaperina—The single known species is found in the Malay Peninsula, Borneo, and the Philippine Islands. It probably occurs in Sumatra as well.

Metaphrynella—The two species are confined to Malaysia, one to Borneo (*sundana*) and one to Sumatra and Malaya (*pollicaris*).

Gastrophrynoides—This monotypic genus is endemic to Borneo.

Microhyla—Three species have been reported from Borneo, four from Sumatra, two from Java, and eight from the Malay Peninsula. Four of the last group occupy larger areas north of Malaysia than in Malaysia. All together, eight species are found in the Indochinese area, one of them, *berdmorei*, having a larger range inside Malaysia.

Only one genus confined to Malaysia, *Phrynella*, does not occur in Borneo.

The family Microhylidae reaches its greatest diversity in the Oriental Region, where 13 genera exist (Parker, 1934). Of the eight genera found in Malaysia, four are endemic and probably autochthonous and a fifth, *Kalophrynus*, has its center of speciation in Malaysia. The center of speciation of *Microhyla* is the Indochinese area where seven species have their main areas of occupation. *Calluella* and *Kaloula* each seem to have had two centers of radiation, one in Malaysia and one north of that area.

RANIDAE: In contrast with the two preceding families, this one has not undergone a radiation at the generic or even subgeneric level in Borneo or the inclusive area of Malaysia. Five genera occur in Borneo and other parts of Malaysia.

Micrixalus—Two species are known from Malaysia, one from Palawan and one from Borneo. Other species are reported from Hainan (Smith, 1923) and India (Myers, 1942).

Ooeidozyga—Interpreted in a broad sense, this genus has two species in Borneo (one endemic), two in the Philippine Islands (one endemic), two in Java and the Malay Peninsula, and one in Sumatra. The species *laevis* is found in all of these areas and as far north as southern China. Several endemic species have been reported from Celebes (Smith, 1927).

Staurois—All three known species occur in Borneo; one of them *natator*, reaches the southern Philippine Islands. The genus is probably autochthonous in Malaysia.

Amolops—The genus has been reported from Malaysia, the Indochinese area, India, and China, usually under the names *Staurois* (*non* Cope) and *Rana*. Adults of three and larvae of six species have been found in Borneo, but no more than two have been collected from any other area except southwestern China.

Rana.—Seventeen species live in Borneo, 16 in Sumatra, 11 in Java, and 27 in Malaya. The total occurring in Malaysia is 36. Thirty-nine species have been found in the Indochinese area, 22 in Thailand and 30 in Indo-China proper. Three of the subgenera recognized by Boulenger (1920) appear in Malaysia, though none is confined to that area. The subgenus *Rana* (*sensu* Boulenger, 1920) is more heterogeneous in the Indochinese area, where six of Boulenger's (1920, pp. 9–10) species groups occur, than in Malaysia where only three are known. The species *Rana hosei*, which does not fit into any of Boulenger's subgenera or species groups, is primarily Malaysian though it ranges into central Thailand.

The family Ranidae does not appear to have had a major center of radiation in Malaysia, though many species are endemic there. Only one small genus, *Staurois*, is confined to parts of Malaysia. The main area of evolution, at levels higher than the species, seems to have been north of the Isthmus of Kra. Movements out of that center account for there being so many more species in the Malay Peninsula than the Greater Sunda Islands; ten of the Malayan species have their main areas of abundance north of the Isthmus of Kra.

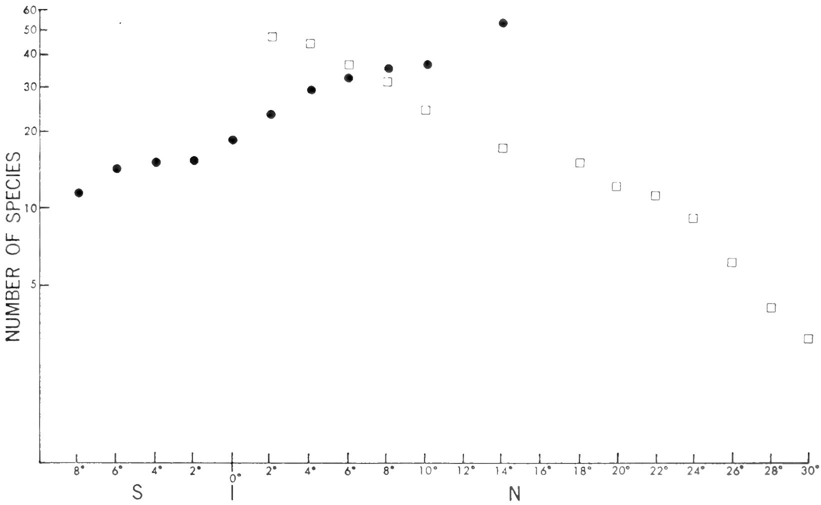


FIG. 67. Changing frequency with latitude of species occurring in Malaysia (open squares) and Indochinese areas (solid circles). Species are placed in these two categories without reference to probable places of origin.

RHACOPHORIDAE: Although Borneo has more species of rhacophorids than any of the other areas in Table 43, the differences between the numbers in Borneo and those of Sumatra or Indo-China are not significant. More species of this family will certainly be described from the Oriental Region, since the tree crown fauna has not been collected systematically.

Rhacophorus—Only one (*leucomystax*) of the 15 species known from Borneo occurs beyond the limits of Malaysia. Endemism within parts of Malaysia is not pronounced. Only five species are confined to Borneo, two to Sumatra (*poecilonotus, modestus*), two to Java (*depressus, javanus*), one to the Malay Peninsula (*robinsoni*), and four to the Philippine Islands (*hecticus, surdus, lissobrachius, emembranatus*). Twelve species occur in several parts of Malaysia.

Another group of ten species is apparently confined to the Indochinese area, except for one (*bimaculatus*) that ranges down into the Malay Peninsula. Thus there seem to be two centers of speciation, one in Malaysia and one in the Indochinese area.

Philautus—Two of the five Bornean species are endemic. The other three are confined to Malaysia.

The frequency of Malaysian[1] species at various latitudes on the

[1] At this point this adjective refers only to presence of a species in the area.

continent diminishes gradually northward at a constant rate until 24° N is reached (fig. 67). The rate of elimination increases at that point and only one species, *Rana limnocharis*, occurs north of 30° N.

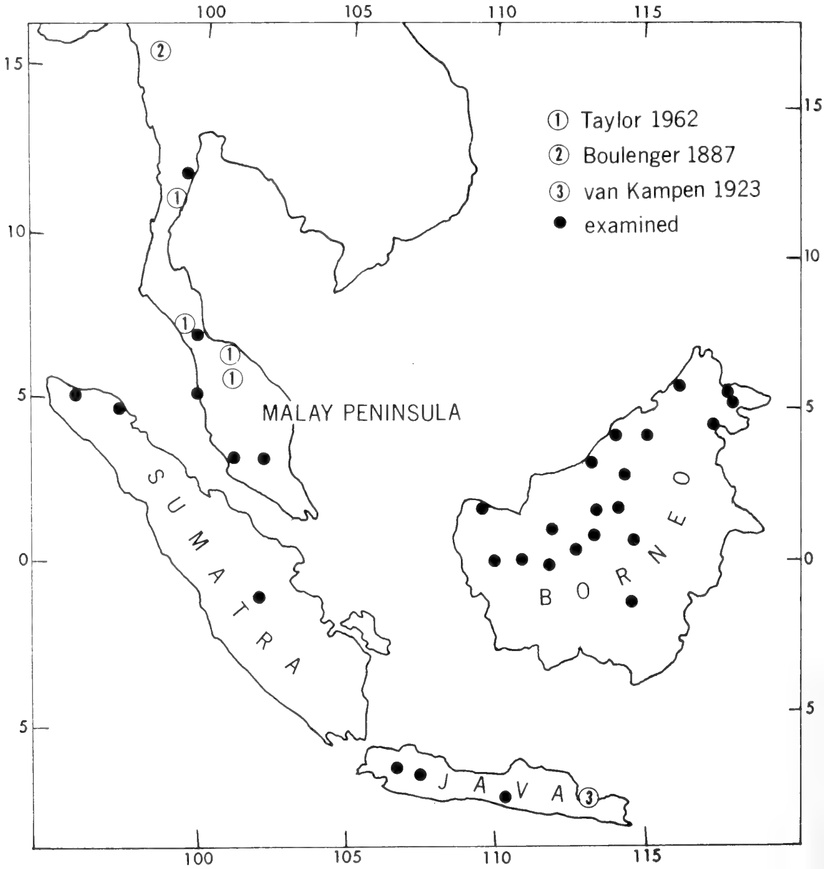


FIG. 68. Distribution of *Bufo asper*.

Species found in the Indochinese area show a similar elimination curve southward: rate of decrease is relatively constant then increases rapidly at 8° S (i.e., southeast of Java). The two curves of fig. 67 have a number of species in common.

Following the analysis of transitional faunas used by Darlington (1957, p. 453), I have divided the amphibians of Malaysia and the Indochinese area into these categories:

Shared species—ranging from at least 20° N (i.e., northern Thailand and North Viet Nam) to 8° S (i.e., into Java): nine species designated in Table 44 by the prefix "shared."

Transitional species probably Malaysian in origin—widely distributed in Sundaland but occurring north to between 13° and 18° N (fig. 68): 5 species ("trans-m" in Table 44). Included here are: *Bufo asper, Pedostibes hosei, Microhyla berdmorei, Rana hosei, Rana cancrivora.*

Transitional species probably Indochinese in origin—ranging from at least 20° N southwards for varying distances, but no farther than 0° (fig. 69): the following 19 species.

Leptobrachium pelodytoides	*R. hascheana*
Bufo macrotis	*R. laticeps*
Calluella guttulata	*R. livida*
Microhyla butleri	*R. macrodactyla*
M. heymonsi	*R. macrognathus*
M. inornata	*R. nigrovittata*
M. ornata	*R. tenasserimensis*
Ooeidozyga lima	*R. tigrina*
Rana alticola	*Philautus asper*
R. cubitalis	

Only one of these species, *R. laticeps,* occurs in Borneo ("trans-i" in Table 44).

Exclusive Malaysian species: 126 ("mal" in Table 44).

Exclusive Indochinese species—may occur in China or Burma, but not south of 12° N: 88.

Questionable species: 3. They occur between 2° and 16° N and thus do not have ranges predominately Indochinese or Malaysian. One of them, *Bufo parvus,* is closely related to the Malaysian species, *B. biporcatus* and *B. quadriporcatus,* and is probably Malaysian in origin. A second, *Megophrys longipes,* belongs to a genus having its principal area of speciation in the Indochinese area. The third species, *Rana doriae,* belongs to a widely distributed species group.

Figure 70 shows elimination curves of the two faunas utilizing species lists based on the preceding categories and omitting the nine shared species. These curves show the same progressive decline in numbers of species away from the faunal centers as the curves of fig. 67. The curves of the two figures also reveal that the faunas change between 8° and 12° N; Smith (1931B) had observed that the

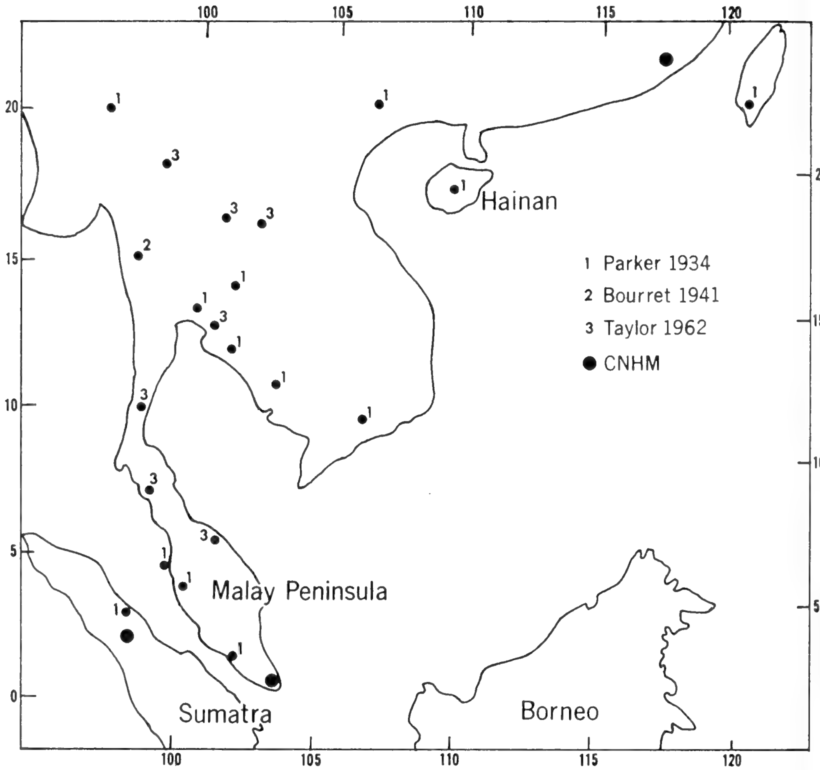


FIG. 69. Distribution of *Microhyla heymonsi*.

faunal boundary lay through the Isthmus of Kra (10° N.) The sharpest relative drop in numbers of Malaysian species takes place between 10° and 12° N and the sharpest drop in Indochinese species at 12°–14° N (fig. 70).

ORIGIN OF MALAYSIAN FAUNA

The peripheral position of Malaysia with respect to the Oriental Region might lead one to expect that its fauna was received in waves from the center of the region, which would be the Burma-Indochina area. Furthermore, the combined area of Burma, Thailand, and Indochina (ca. 700,000 square miles) is considerably larger than the land area of Malaysia (ca. 518,000 square miles),[1] which intro-

[1] Being the combined area of the Malay Peninsula, Borneo, Sumatra, Java, Mindanao, and Palawan. Adding the areas of the smaller islands does not affect the total significantly.

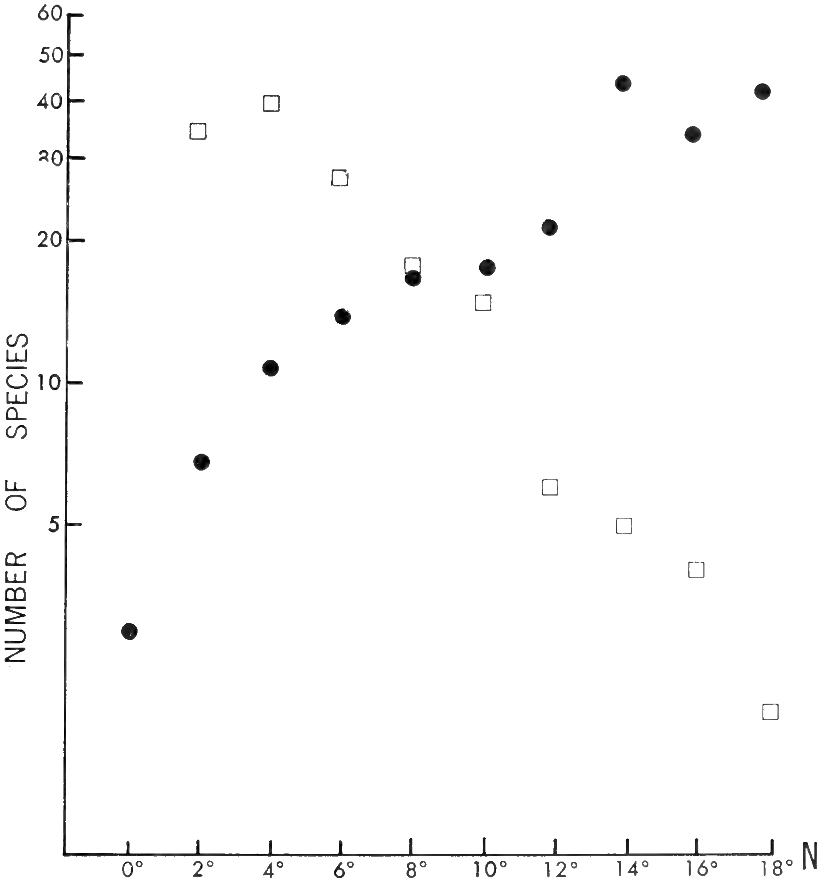


FIG. 70. Changing frequency with latitude of species having Malaysian (open squares) and Indochinese (solid circles) origins, as defined in text.

duces another factor making it likely that Malaysia received its fauna from the area to the north. Darlington (1959) has shown that larger areas tend to have more diverse and larger faunas than do smaller areas and that larger areas tend to be sources of the faunas of adjacent, smaller areas.

The anuran fauna of Malaysia is more diverse than the Burmese-Indochinese fauna (24 genera *vs.* 19) and roughly equal to it in numbers of species (131 Malaysian, 136 Burmese-Indochinese). The present land area of Malaysia represents only a fraction of its extent in the Pleistocene, when most of the South China and Java Seas was

subaerial at least during each glacial period (see p. 10); during those periods the area of Malaysia was probably almost double its present size. The similarity in numbers of species in the Malaysian and Burmese-Indochinese areas is thus not surprising.

The large number of endemic genera or genera with many endemic species in Malaysia (pp. 362–365) suggests that Malaysia has been a faunal source rather than a faunal sink. This is not to say that families of frogs originated in this region, but probably lower taxa did.

Ecological Geography of Bornean Amphibians

As Borneo was until very recently completely covered with forest, it is not surprising that only eight of the Bornean species have been found mainly in large man-made clearings, in towns, and cultivated land: *Bufo melanostictus, Kaloula pulchra, K. baleata, Rana limnocharis, R. cancrivora, R. erythraea, R. nicobariensis,* and *Rhacophorus leucomystax.* Only *R. leucomystax,* of these eight, has been reported from rain forest localities (p. 311). It is therefore appropriate to refer to these eight species as commensals of man. The remainder of the fauna is found mainly in forest, though some species (e.g., *Rhacophorus macrotis, R. pardalis*) are occasionally caught at forest edges.

The fauna as a whole is almost equally divided among aquatic, terrestrial, and arboreal species with very few fossorial ones (Table 45). The habitats of about one-fourth of the species are unknown. Species listed as aquatic in Table 45 are not uniform in habits. A few, such as *Rana kuhli* and *Ooeidozyga laevis,* usually are seen in water or within inches of the water's edge. Others, e.g., *Rana blythi* and *Bufo asper,* are rarely seen in water but are usually on the ground of stream banks anywhere from 0.3–8 m. from the water. *Amolops jerboa, Rana hosei,* and other species, rest on the ground or perch on vegetation along stream banks. None of these species are commonly seen as adults away from stream banks. They differ sharply from species listed as terrestrial or arboreal; species of these last two groups are widely distributed in forest without regard to bodies of water except, in most cases, for breeding purposes. These remarks apply to adults only. Larvae of most species are aquatic.

The frequency distribution of Bornean species in terms of mode of life does not differ appreciably from the distribution of these animals in other areas (Table 46).

The lack of significant difference between the tropical and temperate faunas in Table 46 contrasts markedly with the results of

TABLE 45.—Ecological distribution of Bornean species of amphibians. Adult stage only.

Non-endemic species

Mode of life[1]	Low	Moderate	High	Wide	Unknown	Total
	Altitudinal distribution[1]					
aquatic	4	7	0	6	0	17
terrestrial	4	2	0	6	0	12
arboreal	4	3	1	5	0	13
fossorial	2	0	0	0	0	2
unknown	2	1	2	1	1	7
total	16	13	3	18	1	51

Endemic species

	Low	Moderate	High	Wide	Unknown	Total
aquatic	1	3	1	2	0	7
terrestrial	4	3	0	3	0	10
arboreal	5	1	1	0	0	7
fossorial	2	0	0	0	0	2
unknown	0	3	6	0	5	14
total	12	10	8	5	5	40

[1] See text for explanation of terms.

comparing the mammals of such areas. Davis (1962) finds that terrestrial species make up 52 per cent of the mammalian fauna in lowland forests of Sabah and 72 per cent of the fauna of forest in temperate North America; 45 per cent of the mammals are arboreal in the tropical forest but only 15 per cent are in the temperate forest. The absence of a tropical-temperate dichotomy in the amphibians and the presence of one in the mammals may be related to differences in the abilities of temperate zone representatives of these groups to hibernate and successfully avoid the season of minimal food supply.

Amphibians occur in Borneo from sea level to above 3000 meters. The altitudinal ranges used in Table 45 and elsewhere in this text have the following meanings: low—sea level to 300 meters; moderate—300 to 1000 meters; high—over 1000 meters; wide—ranging from low to high or moderate to high (e.g., 150–1300 m., 600–1500 m.). According to the summary presented by Richards (1952, p. 348), montane rain forest in Malaysia begins at approximately 1000 meters. The mean annual temperature at 1000 m. is roughly 4°–7° C lower than at sea level (*ibid.*, p. 137). Any species confined to elevations below 300 meters is likely to be primarily a swamp forest inhabitant or closely associated with the activities of man. Thus the lowest and highest altitudinal bands have more or less natural bases.

TABLE 46.—Frequency distribution of species of frogs with respect to habitat zones in three areas.

	Borneo		Upemba, Congo[1]		Mississippi[2]	
	Pristine Vegetation					
	tropical rain forest		savanna and deciduous forest		deciduous forest	
	No. of species					
Habitat zone	No.	%	No.	%	No.	%
Aquatic	24	35	18	35	8	35
Terrestrial	21	30	13	25	7	30
Arboreal	20	29	14	27	6	26
Fossorial	4	6	6	12	2	9
total	69[3]		51		23	

[1] Number of species from Schmidt and Inger (1959).

[2] Number of species from Conant (1958). Habitat distribution supplied by C. J. Goin (in litt.).

[3] Omits 21 species whose habits are unknown.

Approximately one-eighth of the species are known only from montane zones (Table 45). The remainder are almost equally divided among the other three altitudinal categories. Three species—*Ansonia fuliginea*, *Pelophryne misera*, and *Philautus aurifasciatus*—have been reported from 3140 meters on Mount Kina Balu (Smith, 1931A, 14, 21), the only Bornean peak exceeding 3000 meters.

How do their ecological distributions affect the geographic ranges of Bornean amphibians? This question is restricted to the species occurring on Borneo only because ecological information from other Malaysian areas is severely limited. In terms of magnitude of geographic ranges, the "shared" species (p. 367) have the greatest ranges, "transitional" species occupying most of one zoogeographic province and part of another have the next largest ranges, Malaysian species living in several parts of this province the third largest ranges, and the species endemic to Borneo the smallest ranges of the species considered. As Table 47 shows, the relationship between extent of geographic range, on the one hand, and altitudinal or habitat distribution, on the other, is almost random.

More of the shared species, that is, the species having the widest geographic ranges, have wide altitudinal ranges, and more of the endemic species are confined to high elevations than one would expect on the basis of chance alone. Organisms having wide altitudinal distributions, in general, have greater ecological valence than those hav-

ing restricted ones, for as species they are at least exposed to a greater range of mean annual temperatures (see above, p. 371).

On the other hand, species confined to high altitudes may have that limitation because of special physiological requirements. They

TABLE 47.—Association between magnitude of geographic range and altitudinal and habitat distributions of Bornean amphibians. Calculated frequencies in italics.

Geographic categories[1]	Altitudinal distribution[2] Low		Moderate		High		Wide		Unknown	Total
Shared	3	*3.0*	1	*2.4*	0	*1.2*	5	*2.4*	0	9
Transitional	3	*2.0*	2	*1.6*	0	*0.8*	1	*1.7*	0	6
Malaysian	10	*11.5*	10	*9.5*	3	*4.5*	12	*9.5*	1	36
Endemic	12	*11.5*	10	*9.5*	8	*4.5*	5	*9.5*	5	40
Total	28		23		11		23		6	91

chi-square[3]=12.74 P=0.18

	Habitat distribution[2] Aquatic		Terrestrial		Arboreal		Fossorial		Unknown	Total
Shared	4	*3.1*	3	*2.8*	1	*2.6*	1	*0.5*	0	9
Transitional	4	*1.7*	0	*1.6*	1	*1.4*	0	*0.3*	1	6
Malaysian	9	*10.3*	9	*9.4*	11	*8.6*	1	*1.7*	6	36
Endemic	7	*8.9*	10	*8.2*	7	*7.4*	2	*1.5*	14	40
Total	24		22		20		4		21	91

chi-square[3]=9.01 P=0.45

[1] Arranged in decreasing order of magnitude. Terms explained in text.
[2] Terms explained in text.
[3] Chi-square tests exclude "unknown" categories.

may be inefficient at the slightly higher temperatures of the lowlands or they may require the usually higher humidities prevalent at high elevations in forested, tropical country (W. H. Brown, 1919, pp. 272–5). If a new land connection arises between areas, it is less likely to have continuously high elevations than a mixture of high and low ones. Consequently, ecological tolerance should have increased the probability for successful dispersal in Malaysia as the physical requirements of a species could have been more easily met.

Fewer arboreal species and more aquatic ones are included in the two most extensive range categories than expected on the basis of chance. However, the departure from random assortment (Table 47) is insignificant.

Habitat distribution of another sort does seem to be correlated with, and is probably causally related to, magnitude of geographic

range. Of the eight species commonly found in large man-made clearings (p. 370), five are "shared" species[1] and form the bulk of that most widely distributed category. Four of these eight species—*Kaloula baleata, Rana limnocharis, R. cancrivora,* and *Rhacophorus leucomystax*—form the bulk (4/7) of the species common to Malaysia and Luzon, the most distant of the Philippine Islands.

The climate of large clearings varies more widely on either a daily or seasonal basis than does the climate within forest (Allee *et al.*, 1949, p. 480 ff.). The maximum daily temperature in clearings in Borneo may be as much as 7° C higher than in the surrounding forest, whereas the minimum temperatures differ by at most 2° C (Inger, 1959). The relative humidity at five feet above ground in a clearing at Deramakot, Sabah varied from 65–98 per cent, whereas at that height in the adjacent forest during the same three-day period the range was 84–98 per cent. At a second station (Bukit Kretam, Sabah) daytime relative humidities during a two-week interval varied from 58 to 82 per cent in the camp clearing and from 71 to 87 per cent in the forest; at this place paired readings were made in clearing and forest 10 minutes apart.

Species that live in the relatively open, modified environments made by man have adaptations, either physiological or behavioral, that enable them to withstand or avoid unfavorable extremes of heat or humidity. These adaptations have probably increased their vagility by increasing the likelihood of tolerable conditions on dispersal routes.

Their close association with man has also increased the probability of their waif dispersal by man. For several of these species, accidental transportation by man is the most likely explanation of their present distribution. *Kaloula pulchra,* for example, is known from Celebes from one locality, the sea port of Makassar (van Kampen, 1923; Parker, 1934). The only authentic Bornean locality for this species is Singkawang (p. 123), also a port. A specimen of *K. pulchra* was found on board a ship loaded with an agricultural product (p. 123). *Rana erythraea* has probably invaded Celebes and the Philippine Islands through accidental transportation by man (Inger, 1954A, p. 484).

The wide geographic distribution of most of the frogs that are commensals of man has a parallel among lizards, such as the house geckos (*Hemidactylus frenatus, Cosymbotus platurus* and *Peropus*

[1] *Bufo melanostictus, Kaloula pulchra, Rana limnocharis, Rana erythraea,* and *Rhacophorus leucomystax.*

mutilatus) and at least one skink (*Mabuya multifasciata*). These lizards occur at many localities in Borneo, but only in towns, villages, and in the case of *Mabuya*, in large, open, man-made clearings. They do not penetrate the rain forest. Their geographic distributions extend from Burma at least to New Guinea (de Rooij, 1915; Smith, 1935).

Another counterpart to these frogs associated with man's activities is found among Melanesian ants. Wilson (1961) observes that the species of ants that have the largest ranges in Melanesia are those that in New Guinea are not conspicuously successful in rain forests, but occur mainly in marginal habitats that support few species. The same species invade virgin rain forest and become dominant in that habitat on smaller islands, such as the Solomon Islands, that have fewer species. In like manner, *Rana cancrivora* and *R. limnocharis* successfully invade forest streams in the Lesser Sundas (Mertens, 1930, pp. 342–3), which have very few species of amphibians.

Factors Limiting the Malaysian Fauna

The factors that ultimately limit the dispersal of tropical amphibians are ecological (temperature, rainfall, vegetation, competition with related animals), geographic (size of areas, distance), and geological (historical events, ocean straits). No one of these factors can account for the limitation of distribution of the Bornean species, but each has had some effect.

Table 48 shows the relationship between number of Bornean species occurring at particular latitudes on the continent and climate. These species are referred to as "Bornean" here only because they occur on the island. To arrive at a more rational and less provincial analysis of what happens on the continent, all of the species found in the Malay Peninsula and the Greater Sunda Islands will be considered.

As already noted (p. 367), the number of Malaysian species drops sharply between 10° and 14° N. coinciding with the development of an extended dry season (Table 48). Beyond that point, the disappearance of Malaysian species is gradual. The vegetation changes in the same narrow belt, but temperature does not (fig. 71). Temperature can therefore be eliminated as an important causal factor in limiting the Malaysian frog fauna at this geographic zone.

In view of the restriction of all but eight Bornean species to rain forest, we may assume that the bulk of the fauna requires constantly

TABLE 48.—Relations between faunal transition, climate, and distance from faunal source in southeastern Asia.

North latitude	Nearest weather station: Place	Nearest weather station: Latitude	Mean temperature (C.) months/year: <22.5°	<20°	<17.5°	Rainfall <50 mm. months/year	Salientian faunas[1] No. of species: Bornean	Malaysian	Indochinese
20°	Haiphong	20° 49′	5	3	1	4.3	10	0	39
18°	Dong Hoi	17° 29′	2	1	0	3.3	13	2	42
16°	—	—	—	—	—	—	13	4	33
14°	Bangkok	13° 45′	0	0	0	4.0	15	5	42
12°	—	—	—	—	—	—	16	6	22
10°	Chumporn	10° 27′	0	0	0	1.0	22	15	18
8°	—	—	—	—	—	—	29	18	17
6°	Kota Baru	6° 10′	0	0	0	1.3	32	28	14
4°	Kuala Lumpur	3° 07′	0	0	0	0.3	37	40	11
2°	Singapore	1° 18′	0	0	0	0	38	35	7

Sources of meteorological data:

Singapore, Kuala Lumpur, Kota Baru—Malayan Meteorological Service, Summary of Observations.
Bangkok, Dong Hoi, Haiphong—World Weather Records 1941–1950, U. S. Dept. Commerce, Weather Bureau.
Chumporn—Monthly Climatic Data for the World, U. S. Weather Bureau.

[1] Bornean=species occurring in Borneo; origins diverse
Malaysian=species with Malaysian origins
Indochinese=species with Indochinese origins

high humidity and moderately high temperatures.[1] These requirements are not satisfied north of the Isthmus of Kra and only few of the Malaysian species are able to tolerate the extended dry season there.

The change from an aseasonal to a seasonal climate north of the Isthmus of Kra is associated with a change in vegetation from evergreen rain forest to deciduous or semi-deciduous forests (fig. 71). As the type of vegetation is dependent on the climate, vegetational change may be merely correlated rather than causally related to distributional limits of amphibians in this region. But vegetation may accentuate or buffer the effects of climate and thus play a contributory role in the distribution of amphibians.

In areas of evergreen tropical rain forest, two weeks may pass without precipitation. Even under those circumstances, however, the humidity in the forest remains at a relatively high level because a canopy of leaves is present offering protection against the sun and wind. For example, during a nine-day interval without rain (April 23 through May 1, 1963) at a camp at Nanga Tekalit, Sarawak, relative humidity in the rain forest at 1.6 meters above ground did not drop below 87 per cent (unpublished data). In the largely deciduous forests of southeastern Asia, the loss of leaves probably exposes the fauna to the full effects of drought.

In general, one expects that, where two faunas meet, the larger of the two will ultimately send more migrants into the range of the smaller than vice versa, all other things being equal. This relationship is a probabilistic one based upon random movements of populations in all directions from their respective centers. In the case in point, however, the movement is greater away from the smaller fauna (Indochinese, see p. 367) suggesting the operation of a selective factor, which is probably climate. A warm, continually humid climate is not likely to act as a barrier to amphibians, whereas drought or cold weather may and probably do prevent dispersal of some species, especially those strictly adapted to rain forest conditions. Hence the greater number of species moving southward, across the Isthmus of Kra, than northward is not surprising.

The general trend, therefore, is for Malaysian amphibians to be limited on the continent to the northward extent of an aseasonal, humid, tropical climate (Afi in the Köppen classification). The ap-

[1] Athough I have no direct ecological observations on the Malayan and Sumatran faunas, I think it reasonable to assume that the same requirements apply to the frogs of those rain forest areas.

pearance of a seasonal climate (Aw in the Köppen classification) acts as a strong filter allowing very few species to pass.

North of the Isthmus of Kra temperature almost certainly is the dominant factor in the continued northward distribution of transitional Malaysian species and the nine species shared by the Malaysian and Indochinese areas. The length of the dry season does not increase appreciably from Bangkok to Hong Kong (Tables 48 and 49). Forest of some sort is present all the way into southern China. Three of the "shared" species—*Rana kuhli*, *Kalophrynus pleurostigma*, and *Leptobrachium hasselti*—are forest inhabitants. Hence, neither the type of vegetation nor the length of the dry season will explain the failure of such species as *Rana hosei*, *Microhyla berdmorei*, and *Pedostibes hosei*, which occur in Thailand, to reach southern China.

TABLE 49.—The relation between climate and northward distribution of amphibians shared[1] by the Malaysian and Indochinese areas.

Weather station		Mean temperature (°C.)			Rainfall	No.
Place	N latitude	<22.5°	<20°	<17.5°	<50 mm.	species
		months/year			mos./yr.	
Hong Kong	22°18′	6	4	3	3.6	9
Amoy	24°28′	6	4.5	3.5	—	7
Wenchow	28°00′	7.5	6	5	—	4
Shanghai	31°15′	8.4	8	6	3.3	1

[1] Shared species are those widely distributed throughout the two areas, which are defined in the text.

The number of months in which the average temperature is below 20° C increases steadily from Bangkok northward into China (Tables 48 and 49). The progressive decline in the number of "shared" tropical species northward in China is directly related to increase in number of cold months (Table 49). The habitat of the commensals of man—*Bufo melanostictus*, *Kaloula pulchra*, *Rana limnocharis*, *Rhacophorus leucomystax*—included in the "shared" category persists as far north as Shanghai. The dry season is no longer at Shanghai than at Dong Hoi, Viet Nam. Competition with congeneric species in China is not a likely explanation for the limitations of these species, as their congeners are more numerous in the tropical areas.

To the east the Malaysian fauna is sharply limited by the Makassar Strait separating Borneo and Celebes. Makassar Strait is today 110 km. wide at its narrowest point. At no time since the Mesozoic has a land connection existed between Borneo and Celebes or be-

tween Java and Celebes (Umbgrove, 1949); Klompe (1961) apparently doubts that Celebes has had a land connection with any of the Greater Sunda Islands since the Paleozoic, if then. During the Pleistocene lowering of the sea level coincident with northern glaciation (Molengraaff and Weber, 1921), the width of this strait was reduced, possibly to as little as 50 km. The shallow Borneo Bank along the east cost of Borneo is less than 55 m. deep (Umbgrove, 1949, fig. 4) and was probably exposed during parts of the Pleistocene.

Only 10 of the species occurring in Malaysia have been reported from Celebes. In addition, the Celebesian fauna includes 12 endemic species and three species (*Rana grunniens, R. modesta,* and *R. papua*) that occur in Celebes, the Moluccas, and other islands to the east. The ten Malaysian species in Celebes are: *Kaloula baleata, K. pulchra, Rhacophorus leucomystax, Rana erythraea, R. cancrivora, R. kuhli, R. microdisca, R. chalconota, Ooeidozyga laevis,* and *Bufo biporcatus*. The first five are commensals of man (p. 370) and hence likely candidates for accidental dispersal. Both *Kaloula pulchra* and *Rana erythraea* have been reported on Celebes only from the port city, Makassar (see also p. 374). *Rana kuhli* and *Ooeidozyga laevis* are distributed from Borneo to China and are presumed to have good powers of dispersal independent of man's activities. The three remaining species (*Rana microdisca, R. chalconota,* and *Bufo biporcatus*) have not been able to disperse northward beyond the Isthmus of Kra.

If we subtract from the Bornean fauna the frogs known on other criteria to be remarkably vagile—either by their own powers or by virtue of association with man—we are left with 80 species, i.e., 91 minus nine "shared" species and two Malaysian commensals of man. Only three (4%) of the 80 have managed to reach Celebes. Thus the Makassar Strait has acted as an effective barrier to Malaysian species lacking special powers of dispersal.

In the south and east, the Malaysian fauna is limited first by climate and then by geographic barriers. Western Java has 34 species of frogs, including all 22 of the species Java shares with Borneo.[1] In Java the heaviest rainfall and shortest dry period occur in the west and the climate becomes noticeably drier in the east (Table 50). Twelve Javan species have not been found in the drier, eastern third (i.e., east of 111° E) of the island. Nine of the species known from

[1] Data on the distributions in Java are taken from van Kampen (1923) except for those of *Ooeidozyga laevis* (Mertens, 1934) and *Kalophrynus pleurostigma* (Mertens, 1957). Excluded are the two species of *Hyla* introduced into Java (Mertens, 1930).

eastern Java[1] have been reported only from high elevations (1200 meters) where presumably the climate is ameliorated by the usual effects of altitude (see above, p. 373). A reduction in number of species eastward in Java has been shown in birds (Mayr, 1944) and in *Calamaria*, burrowing snakes that are mainly rain forest inhabitants (Inger and Marx, 1965).

East of Java the Malaysian frog fauna dwindles in the Lesser Sunda Islands. The drop from Java to Bali is sharp, roughly half of the eastern Javanese fauna failing to cross the narrow (ca. 10 km.) Bali Strait (Table 50). Five more Malaysian species, almost half of the number on Bali, fail to cross the Lombok Strait; they are *Leptobrachium hasselti*, *Bufo melanostictus*, *Microhyla palmipes*, *Rana nicobariensis*, and *R. chalconota*. The number of Malaysian frogs on Lombok, Sumbawa, and Flores remains almost constant (Table 50). One Malaysian species, *Rana macrodon*, is known from Lombok, Sumbawa, and Flores, but has not so far been recorded from Bali (Mertens, 1930).

Changes in climate from eastern Java to Bali and Lombok are not factors in limiting the distribution of Malaysian frogs in this direction. Neither the areas of the islands nor their distances from Java are related in any meaningful way with the total number of species or the number of Malaysian species on the separate islands (Table 50). The vegetation (fig. 71) does not undergo a progressive shift from eastern Java to Bali to Lombok.

The most likely explanation of the limitation of the eastward distribution of the Malaysian fauna in this area is the sea barrier. The kind of species that succeed in crossing the Bali Strait provides some evidence. Six of the species in Bali are commensals of man: *Bufo melanostictus*, *Rana nicobariensis*, *Kaloula baleata*, *Rana cancrivora*, *R. limnocharis*, and *Rhacophorus leucomystax*. The last four occur also on Lombok, Sumbawa, and Flores. I have already suggested that these species are prone to transportation by man (pp. 374, and 379), which could explain their ability to cross each of these narrow straits.

Church (1960B) has evidence that *Bufo melanostictus* has only recently invaded Bali. According to Church, there are no ecological differences between Bali and eastern Java. Yet *melanostictus*, which is extremely common all over Java, was in 1958 confined to the west-

[1] The nine are: *Leptobrachium hasselti*, *Megophrys monticola*, *Cacophryne borbonica*, *Microhyla achatina*, *Rana chalconota*, *Rana microdisca*, *Amolops jerboa*, *Rhacophorus reinwardti*, and *Philautus aurifasciatus*.

TABLE 50.—Relation between climate and number of species of frogs known from Java and the Lesser Sunda Islands.

	Rainfall[1]			Average[2] monthly relative humidity	Area (mi. sq.)	Distance from Java (mi.)	Number of species		
	Total annual mm.	No. of months <100 mm.	No. of months <50 mm.				Malaysian species[3]	Commensals of man	Total fauna
W. Java	1727	4.8	3.2	81.3%	50,745	—	33	7	33
E. Java	1250	6.5	5.6	76.9%		—	21	6	21
Bali	1417	7	2	78.5%	2,243	10	11	6	12
Lombok	1952	4	2	—	1,826	85	7	4	9
Sumbawa	—	—	—	—	5,965	150	6	4	8
Flores	—	—	—	—	5,511	350	7	4	10

[1] Data on Java (Djakarta, 106° 50′ E; Pasaruan, 112° 55′ E) from World Weather Records 1941–1950, U. S. Dept. Commerce, Weather Bureau. Data on Bali and Lombok from Church (1960B).

[2] Data taken from Church (1960B).

[3] In this table the "shared" species (p. 367) are combined with true Malaysian species.

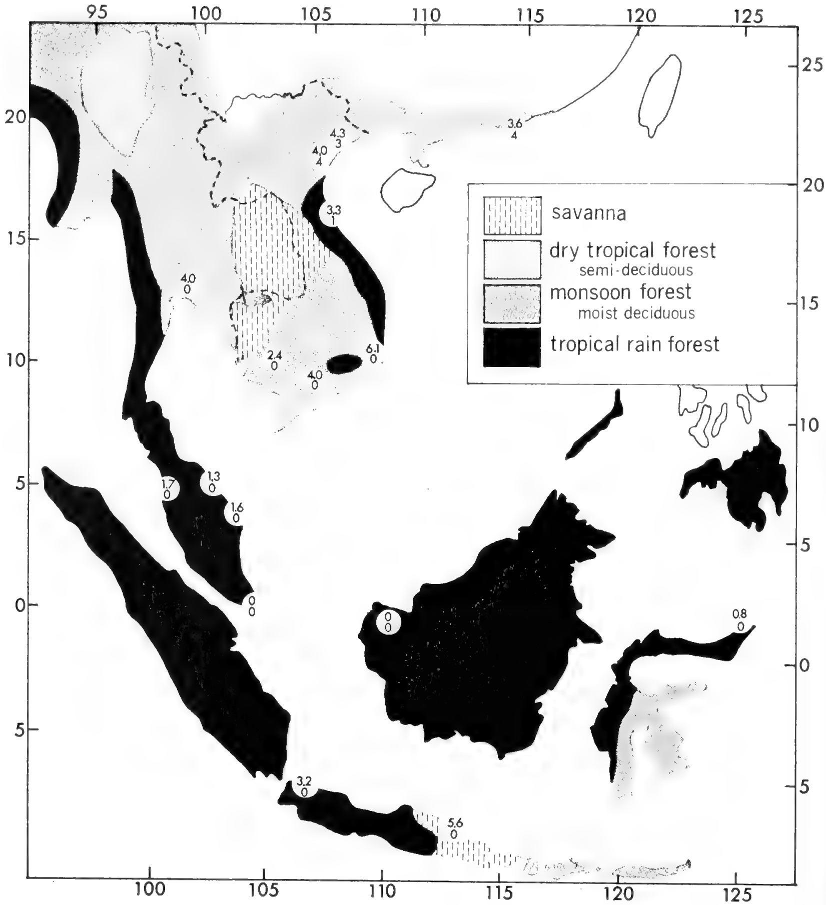


FIG. 71. Southeast Asia and the East Indies. Vegetation distribution from Bartholomew, Times Atlas, 1958, vol. 1, modified slightly according to Richards (1952; fig. 2) and J. H. Davis (1960). Numbers centered over weather stations indicate annual average number of months having less than 50 mm. of rain (upper) and mean temperature below 20° C. (lower).

ern tip of Bali. Only recent arrival can explain the restricted range in Bali.

Only 22 species of Bornean frogs (ca. 25% of the total) occur in the Philippine Islands.[1] The larger of the southern Philippine islands, Mindanao and Palawan, have extensive areas of rain forest and varied

[1] Reasons for considering the direction of dispersal to have been from Borneo to the Philippine Islands are given in Inger, 1954A, pp. 495–6.

topography. They each have far fewer species (34 and 20, respectively) than does Borneo. They thus provide environments in which the Bornean fauna could thrive. Yet only 15 Bornean species are known from Palawan and only 16 from Mindanao.[1] Ecological factors, therefore, do not seem to limit the Malaysian fauna in this direction.

Both Palawan and Mindanao are closer to Borneo (150 and 360 km., respectively) than is Sumatra (400 km.), which has many more (40) Bornean species. Consequently, distance from Borneo does not alone account for the small proportion of the fauna reaching the Philippines.

Throughout the Tertiary the Philippine Islands were apparently separated from all surrounding land masses (van Bemmelen, 1949, summarized in Inger, 1954A). Land connections with Borneo were established in the Pleistocene coincident with Holarctic glaciation. However, the link between the Palawan chain and Borneo was a narrow isthmus and that between Mindanao and Borneo either a narrow isthmus or a series of narrowly separated islands. In each case, the type of connection would have acted as a filter bridge limiting the number of forms that were able to migrate successfully assuming that dispersal is probabilistic and probability of successful dispersal is related to width of an area. Geologic history, therefore, seems to provide the best explanation for the small proportion of Bornean species occurring in the Philippine Islands.

The manner in which these filter bridges operated seems reasonably clear. Drainage patterns on an isthmus are generally perpendicular to the longitudinal axis. This arrangement obtains today on Palawan and the equally narrow Zamboanga Peninsula of Mindanao. Presumably a similar pattern characterized the Pleistocene isthmian links between Borneo, on the one hand, and Palawan and Mindanao, on the other. If this assumption is correct, these isthmian links had drainage patterns that would not have favored dispersal of aquatic or riparian species over long distances. Arboreal and terrestrial species should have had greater chances for successful dispersal to the Philippines than aquatic species that would have been more or less bound to water courses. Analysis of the habits of the Bornean species that reached Palawan and Mindanao reveals this kind of difference (Table 51).

[1] With the exception of *Rana erythraea*, these are the species in Table 44 having the suffix "P."

As the commensals of man apparently have dispersed without regard to land connections (pp. 374 and 379), they can be ignored in this comparison of successful dispersal. Only one species of *Bufo*, the terrestrial species, *biporcatus*, common on the forest floor, has migrated to the Philippines from Borneo. *Bufo asper*, which is one of the most abundant forest amphibians in Borneo, has not; *asper* is strictly riparian. The aquatic forest species common to Borneo and the southern Philippines are *Ooeidozyga laevis*, *Rana signata*, and *Staurois natator*. Conspicuous by their absence from this list are *Rana kuhli*, *R. blythi*, and *R. chalconota*, which are more generally abundant along forest streams in Borneo than *Ooeidozyga laevis* or *Staurois natator*. *Rana signata* is primarily riparian in Borneo though it is occasionally captured at considerable distance from water. About one-third of the arboreal and terrestrial species of Bornean forests have reached Palawan and Mindanao, as compared to only one-seventh of the aquatic forms (Table 51).

TABLE 51.—Relation between habitat and dispersal of frogs from Borneo[1] to the Philippine Islands.

	Forest species		Commensals of man	
Habitat	Borneo	Palawan or Mindanao	Borneo	Palawan or Mindanao
Terrestrial	19	7	1	0
Arboreal	19	6	1	1
Aquatic	20	3	4	3
Fossorial	2	0	2	1

[1] Consideration is limited to those species for which habitat information is available.

The number of Bornean species diminishes northward in the Philippine Archipelago until in Luzon, the most distant and largest of the islands, only seven occur. As suitable habitats and climate are available in Luzon, the most likely explanation for the few species common to Luzon and Borneo is an extension of the explanation for the relatively few Borneo species reaching Palawan. The shortest possible connection between Luzon and Borneo was a long isthmian link (Inger, 1954A, p. 454). Probability for successful dispersal along an isthmus is a function of distance, all other things being equal. Roughly one-sixth (15/91) of the Bornean species succeeded in reaching Palawan, which is 150 km. from Borneo. The probability of dispersal of species from Palawan to Luzon (300 km.) should be less than one-sixth; hence about two of the 15 Bornean species on Palawan

should have reached Luzon. But frogs could have migrated to Luzon via Mindanao. For this route the probabilities are not much different: 16 of 91 Bornean species reached Mindanao, 360 km. from Borneo; the probability for successful dispersal over this distance to a large island was about one-sixth; the distance from Luzon to Mindanao is 360 km.; theoretically fewer than three Bornean species ($16 \times 1/6$) should have reached Luzon via Mindanao.

In fact, seven species are common to Borneo and Luzon: *Kaloula baleata, Rana cancrivora, R. limnocharis, Rhacophorus leucomystax, Ooeidozyga laevis, Rana signata*, and *Rhacophorus pardalis*. The first four are commensals of man (p. 370), which almost certainly disperse at a faster rate and across barriers with greater success than other species. After removal of the commensals of man from the faunal lists, the numbers of Bornean species in the islands leading to Luzon are: Borneo—83; Palawan—11; Mindoro—3; Luzon—2; Samar—5; Leyte—5; Mindanao—13. These numbers fit the stochastic model closely.

In summary, the Malaysian fauna has been limited on the north mainly by the presence of an extended dry season and secondarily by a progressively cooler climate; at the southeast and east mainly by narrow ocean straits; and on the northeast by isthmian bridges that may have been interrupted by narrow ocean straits. It has often been observed (e.g., Darlington, 1957) that the Oriental Region is barrier limited at the south and east. The distribution of the amphibians of Malaysia, which lies at the southeastern extremity of the Oriental Region, illustrate this characteristic very well.

Manuscript accepted for publication June 19, 1964.

REFERENCES

ALCALA, A. C.

1962. Breeding behavior and early development of frogs of Negros, Philippine Islands. Copeia, **1962**, pp. 679–726, 21 figs.

ALCALA, A. C. and W. C. BROWN

1956. Early life history of two Philippine frogs with notes on deposition of eggs. Herpetologica, **12**, pp. 241–246, 2 figs.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, and K. P. SCHMIDT

1949. Principles of animal ecology. xii+837 pp. Philadelphia, W. B. Saunders Co.

ANDERSSON, L. G.

1923. Some reptiles and batrachians from Central Borneo. Nyt Mag. Naturv. Kristiania, **61**, pp. 119–125.

ANNANDALE, NELSON

1906. Notes on the freshwater fauna of India. No. 8—Some Himalayan tadpoles. Jour. Asiatic Soc. Bengal, (N.S.), **2**, pp. 289–292.

1917. Zoological results of a tour in the Far East. Mem. Asiatic Soc. Bengal, **6**, pp. 119–155, pl. 5–6.

1918. Further notes on *Rana tigrina* and allied forms. Rec. Indian Mus., **15**, pp. 59–65, 3 figs.

ANNANDALE, NELSON and S. L. HORA

1922. Parallel evolution in the fish and tadpoles of mountain torrents. Rec. Indian Mus., **24**, pp. 505–509, 2 figs.

BARBOUR, THOMAS

1938. Notes on "*Nectophryne.*" Proc. Biol. Soc. Washington, **51**, pp. 191–195, 1 fig.

BARBOUR, THOMAS and G. K. NOBLE

1916. New amphibians and a new reptile from Sarawak. Proc. New England Zool. Club, **6**, pp. 19–22, pl. 2, 3 text figs.

BARTLETT, EDWARD

1895. Notes on the batrachians or frogs and toads of Borneo and the adjacent islands. Sarawak Note Book, no. 1, pp. 7–14.

BEAUFORT, L. F. DE

1951. Zoogeography of the land and inland waters. viii+208 pp. London, Sidgwick and Jackson, Ltd.

BEDDARD, F. E.

1907. Contributions to the knowledge of the anatomy of the batrachian family Pelobatidae. Proc. Zool. Soc. London, **1907**, pp. 871–911, figs. 229–240.

BEMMELEN, R. W. VAN

1949. The geology of Indonesia. Vol. 1A, General geology of Indonesia and adjacent archipelagoes. xxiii+732 pp., 375 figs. The Hague, Martinus Nijhoff.

BERRY, P. Y. and J. R. HENDRICKSON

1963. *Leptobrachium nigrops*, a new pelobatid frog from the Malay Peninsula, with remarks on the genus *Leptobrachium* in southeastern Asia. Copeia, **1963**, pp. 643–648, 4 figs.

BHADURI, J. L.

1935. The anatomy of the adhesive apparatus in the tadpoles of *Rana afghana* Günther, with special reference to the adaptive modifications. Trans. Roy. Soc. Edinburgh, **58**, pp. 339–349, pl. 58, 3 text figs.

BLAIR, A. P.

1942. Isolating mechanisms in a complex of four species of toads. Biol. Symposia, **6**, pp. 235–249, 2 figs.

1950. Note on Oklahoma microhylid frogs. Copeia, **1950**, p. 152.

BLANFORD, W. T.

1881. On a collection of reptiles and frogs chiefly from Singapore. Proc. Zool. Soc. London, **1881**, pp. 215–227, pls. 20–21.

BLEEKER, PIETER

1858. Eene verzameling reptilien en visschen van Sinkawang (westkust van Borneo). Natuur. Tijd. Ned-Indië, **16**, pp. 188–189.

BOETTGER, OSKAR

1901. Die Reptilien und Batrachier. Kükenthal's wissenschaftliche Reiseergebnisse. Abh. Senck. Ges., **25**, pp. 321–402, pls. 14–16.

BOSCHMA, H.

1922. Über den Trichterapparat der Larven von *Megalophrys montana* Kuhl. Bijdr. tot Dierk., **22**, pp. 9–12, 1 fig.

BOULENGER, G. A.

1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum. xvi+503 pp., 30 pls., London, Taylor & Francis.

1887A. On new batrachians from Malacca. Ann. Mag. Nat. Hist., (5), **19**, pp. 345–348.

1887B. On new reptiles and batrachians from North Borneo. Ann. Mag. Nat. Hist., (5), **20**, pp. 95–97.

1887C. An account of the batrachians obtained in Burma by M. L. Fea, of the Genoa Civic Museum. Ann. Mus. Civ. Genova, (2), **5**, pp. 418–424, pls. 3–5.

1887D. An account of the reptiles and batrachians obtained in Tenasserim by M. L. Fea, of the Genoa Civic Museum. Ann. Mus. Civ. Genova, (2), **5**, pp. 474–486, pls. 6–8.

1889. On the species of *Rhacophorus* confounded under the name of *R. maculatus*. Proc. Zool. Soc. London, **1889**, pp. 27–32, 1 fig.

1890. Second report on additions to the batrachian collection in the natural history museum. Proc. Zool. Soc. London, **1890**, pp. 323–328, pls. 25–26.

1891. Remarks on the herpetological fauna of Mount Kina Baloo, North Borneo. Ann. Mag. Nat. Hist., (6), **7**, pp. 341–345.

1892. An account of the reptiles and batrachians collected by Mr. C. Hose on Mt. Dulit, Borneo. Proc. Zool. Soc. London, **1892**, pp. 505–508, pls. 29–30.

1893A. Descriptions of new reptiles and batrachians obtained in Borneo by Mr. A. Everett and Mr. C. Hose. Proc. Zool. Soc. London, **1893**, pp. 522–528, pls. 42–44.

1893B. Concluding report on the reptiles and batrachians obtained in Burma by Signor L. Fea, dealing with the collection made in Pegu and the Karin Hills in 1887–88. Ann. Mus. Civ. Genova, (2), **13**, pp. 304–347, pls. 7–12.

1894A. On the herpetological fauna of Palawan and Balabac. Ann. Mag. Nat. Hist. (6), **14**, pp. 81–90.

1894B. A list of the reptiles and batrachians collected by Dr. E. Modigliani on Sereinu (Sipora), Mentawei Islands. Ann. Mus. Civ. Genova, (2), **14**, pp. 613–618.

1895. Descriptions of four new batrachians discovered by Mr. Charles Hose in Borneo. Ann. Mag. Nat. Hist., (6), **16**, pp. 169–171.

1899. Descriptions of new batrachians in the collection of the British Museum (Natural History). Ann. Mag. Nat. Hist., (7), **3**, pp. 273–277, pls. 11–12.

1900. Descriptions of new reptiles and batrachians from Borneo. Proc. Zool. Soc. London, **1900**, pp. 182–187, pls. 14–17.

1903. Report on the batrachians and reptiles. Fasc. Malay., Zool., **1**, pp. 131–176, pls. 5–10.

1904. Description of a new genus of frogs of the family Dyscophidae, and list of the genera and species of that family. Ann. Mag. Nat. Hist., (7), **13**, pp. 42–44, pls. 2.

1908. A revision of the oriental pelobatid batrachians (genus *Megalophrys*). Proc. Zool. Soc. London, **1908**, pp. 407–430, pls. 22–25, text fig. 78.

1912. A vertebrate fauna of the Malay Peninsula. Reptilia and Batrachia. xiii+294 pp., 79 figs. London, Taylor and Francis.

1918. Remarks on the batrachian genera *Cornufer*, Tschudi, *Platymantis*, Gthr., *Simomantis*, g.n., and *Staurois*, Cope. Ann. Mag. Nat. Hist. (9), **1**, pp. 372–375.

1920. A monograph of the South Asia, Papuan, Melanesian, and Australian frogs of the genus *Rana*. Rec. Indian Mus., **20**, pp. 1–226.

Bourret, R.

1941. Les batraciens de l'Indochine. x+517 pp., 4 pls., 196 text figs. Institut Océanographique de l'Indochine.

Brongersma, L. D.

1935. Notes on the newly described genus *Cacophryne* Davis. Zool. Meded., **18**, pp. 257–259.

1937. On a small collection of Amphibia from central east Borneo. Zool. Meded., **20**, pp. 6–9, pl. 1.

Brown, A. E.

1902. A collection of reptiles and batrachians from Borneo and the Loo Choo Islands. Proc. Acad. Nat. Sci. Philadelphia, **1902**, pp. 175–186.

Brown, W. H.

1919. Vegetation of Philippine mountains. 434 pp., 41 pls., 30 text figs. Manila, Bur. of Printing.

Brown, W. L. and E. O. Wilson

1955. Character displacement. Syst. Zool., **5**, pp. 49–64, 6 figs.

Butler, A. L.

1904. A list of the batrachians known to inhabit the Malay Peninsula, with some remarks on their habits, distribution, etc. Jour. Bombay Nat. Hist. Soc., **15**, pp. 387–402.

Cochran, D. M.

1926. A new pelobatid batrachian from Borneo. Jour. Washington Acad. Sci., **16**, pp. 446–447.

Church, Gilbert

1959. Size variation in *Bufo melanostictus* from Java and Bali. Treubia, **25**, pp. 113–126.

1960A. Annual and lunar periodicity in the sexual cycle of the Javanese toad, *Bufo melanostictus* Schneider. Zool., **44**, pp. 181–188, 1 pl.

1960B. The invasion of Bali by *Bufo melanostictus*. Herpet., **16**, pp. 15–22.

1960C. A comparison of a Javanese and a Balinese population of *Bufo biporcatus* with a population from Lombok. Herpet., **16**, pp. 23–28.

CONANT, ROGER

1958. A field guide to reptiles and amphibians of the United States and Canada east of the 100th meridian. xv+366 pp., 40 pls., 62 text figs.

COPE, E. D.

1865. Sketch of the primary groups of Batrachia Salientia. Nat. Hist. Rev., **1865**, pp. 97–120.

DARLINGTON, P. J.

1957. Zoogeography: the geographical distribution of animals. xi+675 pp., 80 figs.

1959. Area, climate, and evolution. Evolution, **13**, pp. 488–510, 8 figs.

DAVIS, D. D.

1935. A new generic and family position for *Bufo borbonica*. Field Mus. Nat. Hist., Zool. Ser., **20**, pp. 87–92, fig. 8.

1962. Mammals of the lowland rain-forest of North Borneo. Bull. Nat. Mus. Singapore, no. 31, pp. 1–129, 23 pls., 19 text figs.

DAVIS, J. H.

1960. The forests of Burma. 23 pp., 10 figs. Gainesville, Fla., Univ. of Florida.

DUNN, E. R.

1928. Results of the Douglas Burden Expedition to the Island of Komodo. IV.—Frogs from the East Indies. Amer. Mus. Novit., no. 315, 9 pp.

FLOWER, S. S.

1896. Notes on a collection of reptiles and batrachians made in the Malay Peninsula in 1895–96; with a list of the species recorded from that region. Proc. Zool. Soc. London, **1896**, pp. 856–914, pls. 44–46.

1899. Notes on a second collection of batrachians made in the Malay Peninsula and Siam, from November 1896 to September 1898, with a list of the species recorded from those countries. Proc. Zool. Soc. London, **1899**, pp. 885–916, pls. 59–60.

GRIFFITHS, IVOR

1959. The phylogeny of *Sminthillus limbatus* and the status of the Brachycephalidae. Proc. Zool. Soc. London, **132**, pp. 457–487, 4 pls., 18 text figs.

1963. The phylogeny of the Salientia. Biol. Rev., **38**, pp. 241–292.

GÜNTHER, ALBERT

1895. The reptiles and batrachians of the Natuna Islands. Novit. Zool., **2**, pp. 499–502.

HALDANE, J. B. S.

1954. The biochemistry of genetics. 144 pp. London, George Allen and Unwin, Ltd.

HOOGSTRAAL, HARRY

1951. Philippine Zoological Expedition, 1946–1947. Narrative and itinerary. Fieldiana, Zool., **33**, pp. 1–86, 7 pls., 7 text figs.

INGER, R. F.

1954A. Systematics and zoogeography of Philippine Amphibia. Fieldiana, Zool., **34**, pp. 389–424, figs. 85–91.

1954B. On a collection of amphibians from Mount Kina Balu, North Borneo. Jour. Washington Acad. Sci., **44,** pp. 250–251.

1956. Some amphibians from the lowlands of North Borneo. Fieldiana, Zool., **34,** pp. 389–424, figs. 85–91.

1958. A note on the Philippine frogs related to *Rana macrodon.* Fieldiana, Zool., **39,** pp. 253–255.

1959. Temperature responses and ecological relations of two Bornean lizards. Ecology, **40,** pp. 127–136, 4 figs.

1960A. Notes on toads of the genus *Pelophryne.* Fieldiana, Zool., **39,** pp. 415–418, fig. 72.

1960B. A review of the oriental toads of the genus *Ansonia* Stoliczka. Fieldiana, Zool., **39,** pp. 473–503, figs. 81–91.

1964. Two new species of frogs from Borneo. Fieldiana: Zool., **44,** pp. 151–159.

INGER, R. F. and P. K. CHIN

1962. The freshwater fishes of North Borneo. Fieldiana, Zool., **45,** pp. 1–268, 120 figs.

INGER, R. F. and BERNARD GREENBERG

1956. Morphology and seasonal development of sex characters in two sympatric African toads. Jour. Morph., **99,** pp. 549–574, 11 figs.

INGER, R. F. and N. S. HAILE

1959. Two new frogs from Sarawak. Sarawak Mus. Jour., **9**, pp. 270–276. 4 figs.

INGER, R. F. and H. MARX

1965. The systematics and evolution of the Oriental colubrid snakes of the genus *Calamaria.* Fieldiana, Zool., **49,** 1–304.

KAMPEN, P. N. VAN

1905. Amphibien von Palembang (Sumatra). Zool. Jahrb., (Syst.), **22,** pp. 701–716, pl. 26.

1907. Amphibien des indischen Archipels. Zool. Ergebn. Reise Niederl. Ost-Indien, **4,** pp. 383–416, pl. 16.

1910A. Eine neue *Nectophryne*-Art und andere Amphibien von Deli (Sumatra). Nat. Tijd. Ned.-Indië, **69,** pp. 18–24, 1 pl.

1910B. Beitrag zur Kenntnis der Amphibienlarven des indischen Archipels. Nat. Tijd. Ned.-Indië, **69,** pp. 25–48, 1 pl.

1923. The Amphibia of the Indo-Australian Archipelago. xii+304 pp., 29 figs., Leiden, E. J. Brill, Ltd.

KIRTISINGHE, P.

1946. The presence in Ceylon of a frog with direct development on land. Ceylon Jour. Sci., B., **23,** pp. 109–112.

KLOMPE, T. H. F.

1961. Pacific and Variscian orogeny in Indonesia. A structural synthesis. Proc. 9th Pacific Sci. Congr., **12,** pp. 76–115, 15 figs.

KUENEN, P. H.

1950. Marine geology. x+568 pp., 246 figs., 1 map. New York, John Wiley and Sons.

LAIDLAW, F. F.

1900. On the frogs collected during the "Skeat Expedition" to the Malay Peninsula, 1899–1900. Proc. Zool. Soc. London, **1900,** pp. 883–890, pl. 57.

LIMBAUGH, B. A. and E. P. VOLPE
1957. Early development of the Gulf Coast Toad, *Bufo valliceps* Wiegmann. Amer. Mus. Novit., no. 1842, 32 pp.

LIU, C. C.
1935. Types of vocal sac in the Salientia. Proc. Boston Soc. Nat. Hist., **41**, pp. 19–40, pls. 4–8.
1950. Amphibians of West China. Fieldiana, Zool. Mem., **2**, pp. 1–400, 10 pls., 100 text figs.

MAYR, ERNST
1944. Wallace's Line in the light of recent zoogeographic studies. Quart. Rev. Biol., **19**, pp. 1–14, 2 figs.

MERTENS, ROBERT
1930. Die Amphibien und Reptilien der Inseln Bali, Lombok, Sumbawa, und Flores. Abh. Senck. Naturf. Ges., **42**, pp. 115–344, 9 pls.
1934. Die Amphibien und Reptilien der deutschen limnologischen Sunda-Expedition. Arch. Hydrob., Suppl. Band **12**, Tropische Binnengewässer, **4**, pp. 677–701.
1957. Amphibien und Reptilien aus dem äussersten westen Javas und von benachbarten Eilanden. Treubia, **24**, pp. 83–105, 1 fig.

MOCQUARD, F.
1890. Recherches sur la faune herpetologique des Iles de Bornéo et de Palawan. Nouv. Arch. Mus. Nat. Hist. Nat., (3), **2**, pp. 115–168, pls. 7–11.
1892. Nouvelle contribution à la faune herpetologique de Bornéo. Mem. Soc. Zool. France, **5**, pp. 190–206, pl. 7.

MOLENGRAAFF, G. A. F. and MAX WEBER
1921. On the relation between the Pleistocene glacial period and the origin of the Sunda Sea (Java and South China Sea), and its influence on the distribution of coral reefs and on the land and fresh-water fauna. Proc. Akad. Wetens. Amsterdam, **23**, pp. 395–447, 3 figs.

MYERS, G. S.
1942. A new frog of the genus *Micrixalus* from Travancore. Proc. Biol. Soc. Washington, **55**, pp. 71–74.

MYERS, G. S. and A. E. LEVITON
1962. Generic classification of the high-altitude pelobatid toads of Asia (*Scutiger*, *Aelurophryne*, and *Oreolalax*). Copeia, **1962**, pp. 287–291.

NOBLE, G. K.
1927. The value of life history data in the study of the evolution of the Amphibia. Ann. N. Y. Acad. Sci., **30**, pp. 31–128, pl. 9, 30 text figs.
1931. The biology of the Amphibia. xiii+577 pp., 174 figs. New York, McGraw-Hill Publ. Co., Inc.

PARKER, H. W.
1934. A monograph of the Microhylidae. viii+208 pp., 67 figs. London, Jarrold & Sons, Ltd.

PARKER, H. W. and E. R. DUNN
1964. Dentitional metamorphosis and the Amphibia. Copeia, **1964**, pp. 75–86.

PETERS, WILHELM
1872. Übersicht der von den Herren Mse. G. Doria und Dr. O. Beccari in Sarawak auf Borneo von 1865 bis 1868 gesammelten Amphibien. Ann. Mus. Civ. Genova, **3**, pp. 29–45, pls. 2–6.

Pope, C. H.

1931. Notes on amphibians from Fukien, Hainan, and other parts of China. Bull. Amer. Mus. Nat. Hist., **61**, pp. 397–611, pls. 13–22, 39 text figs.

Pope, C. H. and A. M. Boring

1940. A survey of Chinese Amphibia. Peking Nat. Hist. Bull., **15**, pp. 13–86.

Reinhard, Max and Eduard Wenk

1951. Geology of the Colony of North Borneo. Geol. Surv. Dept., Brit. Terr. Borneo, Bull. 1, xiv+160 pp., 20 pls., 29 text figs.

Richards, P. W.

1952. The tropical rain forest. xviii+450 pp., 15 pls., 43 text figs. Cambridge Univ. Press.

Rooij, Nelly de

1915. The reptiles of the Indo-Australian Archipelago. I. xiv+384 pp., 132 figs.

Roux, Jean

1906. Synopsis of the toads of the genus *Nectophryne*. B. & P., with special remarks on some known species and description of a new species from German East Africa. Proc. Zool. Soc. London, **1906**, pp. 58–65, pl. 2.

Schijfsma, K.

1932. Notes on some tadpoles, toads and frogs from Java. Treubia, **14**, pp. 43–72, 8 figs.

Schmidt, K. P. and R. F. Inger

1959. Amphibians. Explor. Parc Nat. Upemba, Fasc. 56, pp. 1–264.

Shumway, W.

1940. Stages in the normal development of *Rana pipiens:* I. External form. Anat. Rec., **78**, pp. 139–148.

Siegel, Sidney

1956. Nonparametric statistics for the behavioral sciences. xvii+312 pp. New York, McGraw-Hill Book Co., Inc.

Smith, M. A.

1916A. Descriptions of five tadpoles from Siam. Jour. Nat. Hist. Soc. Siam, **2**, pp. 37–43, 2 pls.

1916B. On a collection of reptiles and batrachians from Peninsular Siam. Jour. Nat. Hist. Soc. Siam, **2**, pp. 148–175, 1 pl.

1917. On tadpoles from Siam. Jour. Nat. Hist. Soc. Siam, **2**, pp. 261–275, 2 pls.

1921A. New or little-known reptiles and batrachians from southern Annam (Indo-China). Proc. Zool. Soc. London, **1921**, pp. 423–440, 2 pls.

1921B. Two new batrachians and a new snake from Borneo and the Malay Peninsula. Jour. Fed. Malay States Mus., **10**, pp. 197–199, pl. 2.

1922. On a collection of reptiles and batrachians from the mountains of Pahang, Malay Peninsula. Jour. Fed. Malay States Mus., **10**, pp. 263–282.

1923. On a collection of reptiles and batrachians from the Island of Hainan. Jour. Nat. Hist. Soc. Siam, **6**, pp. 195–212, 4 figs.

1925A. On a collection of reptiles and amphibians from Mt. Murud, Borneo. Sarawak Mus. Jour., **3**, pp. 5–14, 1 pl.

1925B. Contributions to the herpetology of Borneo. Sarawak Mus. Jour., **3**, pp. 15–34, 1 fig.

1926. The function of the "funnel" mouth of the tadpoles of *Megalophrys*, with a note on *M. aceras* Boulenger. Proc. Zool. Soc. London, **1926**, pp. 983–988, 2 figs.

1927. Contributions to the herpetology of the Indo-Australian Region. Proc. Zool. Soc. London, **1927**, pp. 199–225, 2 pls., 4 text figs.

1930. The Reptilia and Amphibia of the Malay Peninsula. Bull. Raffles Mus., no. 3, pp. 1–149, 13 figs.

1931A. The herpetology of Mt. Kinabalu, North Borneo, 13,455 ft. Bull Raffles Mus., no. 5, pp. 3–32, 2 pls., 3 text figs.

1931B. The fauna of British India. Reptilia and Amphibia. I. xvi + 185 pp., 2 pls., 42 text figs. London, Taylor and Francis.

1935. *Ibid.* II. xiii+406 pp., 1 pl., 94 text figs.

1940. The amphibians and reptiles obtained by Mr. Ronald Kaulback in Upper Burma. Rec. Indian Mus., **42**, pp. 465–486, pl. 8.

SMYTHIES, B. E.

1957. An annotated checklist of the birds of Borneo. Sarawak Mus. Jour., **7**, pp. 523–818.

STEJNEGER, LEONHARD

1925. Chinese amphibians and reptiles in the United States National Museum. Proc. U.S. Nat. Mus., **66**, pp. 1–115, 4 figs.

TAYLOR, A. C. and J. J. KOLLROS

1946. Stages in the normal development of *Rana pipiens* larvae. Anat. Rec., **94**, pp. 7–24, 5 pls., 1 text fig.

TAYLOR, E. H.

1920. Philippine Amphibia. Philippine Jour. Sci., **16**, pp. 213–359, 10 pls., 9 text figs.

1922A. Additions to the herpetological fauna of the Philippine Islands, I. Philippine Jour. Sci., **21**, pp. 161–206, 7 pls.

1922B. Idem., II. Philippine Jour. Sci., **21**, pp. 257–303, 4 pls.

1923. Idem. III. Phillipine Jour. Sci., **22**, pp. 515–557, 3 pls.

1960. On the caecilian species *Ichthyophis monochrous* and *Ichthyophis glutinosus* and related species. Univ. Kansas Sci. Bull., **40**, pp. 37–120, 38 figs.

1962. The amphibian fauna of Thailand. Univ. Kansas Sci. Bull., **43**, pp. 265–599, 107 figs.

TIHEN, J. A.

1960. Two new genera of African bufonids, with remarks on the phylogeny of related genera. Copeia, **1960**, pp. 225–233, 1 fig.

TREWAVAS, ETHELWYNN

1933. The hyoid and larynx of the Anura. Phil. Trans. Roy. Soc. London, (B), **222**, pp. 401–527, 82 figs.

UMBGROVE, J. H. F.

1949. Structural history of the East Indies. xi+63 pp., 10 pls., 68 text figs. Cambridge Univ. Press.

WILSON, E. O.

1961. The nature of the taxon cycle in the Melanesian ant fauna. Amer. Nat., **95**, pp. 169–193.

WITTE, G. F. DE

1933. Liste des batraciens et des reptiles d'extreme-orient et des Indes orientales récueillis, en 1932, par S. A. R. le Prince Léopold de Belgique. Bull. Mus. Roy. Hist. Nat. Belgique, **9**, no. 24, pp. 1–8.

WOLF, SIEGFRIED

1936. Revision der Untergattung *Rhacophorus*. Bull. Raffles Mus., no. 12, pp. 137–217, 8 figs.

ZELLER, CHRISTOPH

1960. Das periodische Eierlegen des Klatterfrosches *Rhacophorus leucomystax* (Kuhl). Rev. Suisse Zool., **67**, pp. 303–308, 2 figs.

INDEX

Principal taxonomic discussion indicated by **bold-faced** type.

Publication 1012